THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

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# VERTEBRATA

ARTICLE 7
Pages 1-92, Figures 1-131

## EARLY MIOCENE RODENTS AND INSECTIVORES FROM NORTHEASTERN COLORADO

By Robert W. Wilson

ARTICLE 8
Pages 1-24, Figures 1-21

## A NEW ARMORED DINOSAUR FROM THE CRETACEOUS OF KANSAS

By Theodore H. Eaton, Jr.

ARTICLE 9
Pages 1-32, Plate 1, Figures 1-32

## OSTEOLOGY OF MYLAGAULUS LAEVIS, A FOSSORIAL RODENT FROM THE UPPER MIOCENE OF COLORADO

By Sylvia Robinson Fagan

(Contributions from the Museum of Natural History)

The University of Kansas Publications

November 21, 1960

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LAWRENCE

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# EARLY MIOCENE RODENTS AND INSECTIVORES FROM NORTHEASTERN COLORADO

By ROBERT W. WILSON
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CONTENTS

| | PAGE |
|---|---|
| ABSTRACT | 5 |
| INTRODUCTION | 5 |
| Acknowledgments | 5 |
| Recovery methods | 6 |
| OCCURRENCE OF FOSSILS | 6 |
| Ecology of Quarry A | 7 |
| GEOLOGIC AGE AND CORRELATION OF FAUNA | 13 |
| DESCRIPTION AND DISCUSSION OF FOSSIL VERTEBRATES | 19 |
| Lower Vertebrates | 19 |
| Higher Vertebrates | 19 |
| Class Mammalia | 19 |
| Order Insectivora | 20 |
| Superfamily Erinaceioidea | 21 |
| Family Erinaceidae | 21 |
| *Metechinus* sp., cf. *M. marslandensis* Meade, 1941 | 21 |
| Superfamily Soricoidea | 21 |
| ?Family Metacodontidae | 21 |
| *Plesiosorex coloradensis* Wilson, n. sp. | 21 |
| *Plesiosorex?* sp. (small form) | 27 |
| Family Soricidae | 27 |
| Subfamily Heterosoricinae | 27 |
| *Heterosorex roperi* Wilson, n. sp. | 27 |
| *Heterosorex?* sp. | 33 |
| Subfamily Soricinae | 33 |
| *Sorex vireti* Wilson, n. sp. | 33 |
| *Sorex compressus* Wilson, n. sp. | 35 |
| Comparisons | 37 |
| Family Talpidae | 38 |
| Subfamily Scalopinae | 38 |
| Genus *Mydecodon* Wilson, n. gen. | 38 |
| *Mydecodon martini* Wilson, n. sp. | 38 |
| Genus *Scalopoides* Wilson, n. sp. | 42 |
| *Scalopoides isodens* Wilson, n. sp. | 42 |
| *Proscalops* sp., cf. *P. secundus* Matthew, 1909 | 46 |
| *Proscalops?* sp. | 48 |
| Soricoid sp. indet. | 49 |
| Order Lagomorpha | 49 |
| Family Leporidae | 49 |
| *Hypolagus?* sp. | 49 |
| Family Ochotonidae | 49 |
| *Oreolagus* nr. *O. nebrascensis* Galbreath, 1953 | 49 |
| Order Rodentia | 51 |
| Suborder Sciuromorpha | 51 |
| Family Mylagaulidae | 51 |
| *Mesogaulus paniensis* (Matthew, 1902) | 51 |
| Family Sciuridae | 57 |
| *Palaeoarctomys? bryanti* Wilson, n. sp. | 57 |
| *Sciurus* sp. A | 62 |
| *Sciurus* sp. B | 63 |
| Remarks on Fossil Sciuridae | 63 |
| Suborder Castorimorpha | 65 |
| Family Castoridae | 66 |
| *Anchitheriomys?* sp. | 66 |
| *Monosaulax,* n. sp. | 68 |
| Remarks on Fossil Castorids | 70 |
| Suborder Myomorpha | 72 |
| Superfamily Geomyoidea | 72 |
| Family Eomyidae | 72 |
| *Pseudotheridomys hesperus* Wilson, n. sp. | 72 |
| Family Heteromyidae | 75 |
| *Proheteromys sulculus* Wilson, n. sp. | 75 |
| *Florentiamys?* sp. | 78 |
| *Mookomys* sp., cf. *M. formicorum* Wood, 1935 | 78 |
| *Proheteromys* sp., cf. *P. magnus* Wood, 1935 | 79 |
| Subfamily Entoptychinae | 81 |
| Superfamily Dipodoidea | 81 |
| Family Zapodidae | 81 |
| *Plesiosminthus (Plesiosminthus) clivosus* Galbreath, 1953 | 81 |
| *Plesiosminthus (Schaubeumys) galbreathi* Wilson, n. sp. | 83 |
| Relationships of *Schaubeumys* | 85 |
| REFERENCES | 88 |

## ILLUSTRATIONS


| FIGURE | | PAGE |
|---|---|---|
| 1. | Graph comparing avian faunas of McKittrick and Fossil Lake | 10 |
| 2. | Graph of skeletal elements per individual plotted against number of species for McKay mammalian fauna | 11 |
| 3. | Graph of skeletal elements per individual plotted against number of species for Hemphill mammalian fauna | 11 |
| 4. | Correlation of Quarry A with other local rock units, and its fauna with standard North American provincial ages | 13 |
| 5. | Some proposed correlations of the North American provincial ages with European standards | 14 |
| 6. | Stratigraphic ranges of some European mammals | 15 |
| 7. | Suggested stratigraphic correlation of some North American and European fossil faunas | 16 |
| 8. | Stratigraphic ranges in Europe of mammalian genera also present at Quarry A | 17 |
| 9-10. | *Plesiosorex coloradensis,* skull fragment, and occlusal view of left $M^2$ | 22 |
| 11-13. | *Plesiosorex coloradensis,* lower jaws and lower teeth | 23 |
| 14-20. | *Heterosorex roperi,* upper jaws and teeth | 28 |
| 21. | *Heterosorex roperi,* type specimen | 29 |
| 22. | *Heterosorex roperi,* lower jaw | 30 |
| 23-26. | *Sorex vireti,* lower jaws and teeth | 34 |
| 27-28. | *Sorex vireti,* teeth | 35 |
| 29-30. | *Sorex compressus,* upper and lower jaws | 36 |
| 31. | *Sorex compressus,* left lower jaw | 37 |
| 32-33. | *Mydecodon martini,* lower jaws | 39 |
| 34-38. | *Scalopoides isodens,* lower jaws and teeth | 43 |
| 39. | *Scalopoides isodens,* humerus | 44 |
| 40. | Graph of ratio of length of humerus to length of lower molar series in several fossil moles | 45 |
| 41-46. | *Proscalops* sp., cf. *P. secundus,* teeth | 47 |
| 47-59. | *Mesogaulus paniensis,* occlusal views of teeth | 52 |
| 60-67. | *Palaeoarctomys? bryanti,* and *Sciurus,* jaws and teeth | 58 |
| 68-70. | *Anchitheriomys?* sp., skull fragment and teeth | 66 |
| 71-80. | *Monosaulax,* n. sp., upper jaw and upper teeth | 69 |
| 81-95. | *Monosaulax,* n. sp., lower jaw and lower teeth | 70 |
| 96-101. | *Pseudotheridomys hesperus,* jaws and teeth | 73 |
| 102-114. | *Proheteromys sulculus,* jaws and teeth | 76 |
| 115-120. | *Florentiamys?* sp. and *Mookomys* sp., cf. *M. formicorum,* lower jaw and teeth | 78 |
| 121-125. | *Proheteromys* sp., cf. *P. magnus,* teeth | 79 |
| 126. | *Plesiosminthus clivosus,* right upper jaw fragment | 81 |
| 127-130. | *Plesiosminthus galbreathi,* upper jaw fragments, and upper incisor | 84 |
| 131. | *Plesiosminthus galbreathi,* type specimen | 84 |

## ABSTRACT

A sparse fauna of Marslandian (late Early Miocene) age has been known from the lower part of the Pawnee Creek Formation of northeastern Colorado for over fifty years. The Martin Canyon area of Logan County has produced most of the known fossils, and University of Kansas (Museum of Natural History) field parties have obtained specimens from outcrops in this place.

At one locality in Martin Canyon a small excavation, named Quarry A, produced a number of fragmentary specimens of insectivores, lagomorphs, and rodents; these specimens, obtained in 1950-52, are the subject of the present report.

The several hundred specimens of small mammals from Quarry A represent twelve species of Insectivora, two species of Lagomorpha, and fourteen species of Rodentia. Of these, six species of insectivores and four species of rodents are new and described herein. An outstanding feature of Quarry A is the discovery of several genera previously unknown, or not certainly known, outside of Eurasia. These are: *Plesiosorex, Heterosorex, Pseudotheridomys,* and *Plesiosminthus.*

The fauna from Quarry A seemingly represents a Miocene riparian-fluvial association.


## INTRODUCTION

In the summer of 1950, a field party of the Museum of Natural History, University of Kansas, opened an excavation in the lower part of the Pawnee Creek Formation of northeastern Colorado in a search for fossil vertebrates. Only a few days were spent at this time in working the site, but it was even then obvious that an important site for small mammals had been found. The results of this brief period of work was reported by GALBREATH (1953) in a contribution to the geology and paleontology of northeastern Colorado.

Subsequently, the locality was worked for approximately a month in each of the summers of 1951 and 1952. Many of the smaller specimens were found, however, not in the field during quarry operations, but in the laboratory by careful searching of matrix brought in each summer at the conclusion of the season.

As recovery of specimens proceeded, it became obvious that several of the smaller mammals were not only new records, but that a most unexpected relationship to European species existed. Recognition of this Old World element caused study of the collection to be postponed until a proper investigation could be made.

In the academic year 1956-57 I took the Colorado specimens to Europe and directly compared them with European material. The present report is the result.


### ACKNOWLEDGMENTS

Numerous persons and institutions have aided me materially in the studies leading to the present work. I wish to thank first the Board of Regents, University of Kansas, for granting me sabbatical leave, 1956-57, and the Trustees of the John Simon Guggenheim Memorial Foundation for the award of a Fellowship for study abroad.

I thank also the officials of the British Museum (Natural History), and especially Dr. E. I. WHITE, Keeper of Geology, and Dr. A. TINDELL HOPWOOD for providing me with all necessary facilities of space and equipment during my long sojourn at the Natural History Museum, as well as for complete freedom to use the collections and library. Others abroad who opened the collections under their care to me, and who were most hospitable in every conceivable way are: Abbé RENE LAVOCAT, École Pratique des Hautes Études; Dr. JEAN VIRET, University of Lyon and Museum of Natural History of the City of Lyon, France; and Dr. SAMUEL SCHAUB and Dr. JOHANNES HÜRZELER, Natural History Museum of Basel, Switzerland. I thank also Dr. GEORGE G. SIMPSON, then of the American Museum of Natural History, for permission to study specimens under his care.

The field and laboratory work that led to the assembling of the Quarry A collection, as it came to be known, also produced its full quota of debts on my part to various individuals now or at one time members of the University of Kansas community. First and foremost, I am greatly indebted to my long-time friend and colleague, Dr. EDWIN C. GALBREATH, now of the University of Southern Illinois. He actively participated in all three seasons of field work, led the expedition in 1951, and more than any other individual was responsible for the large number of specimens found in the laboratory. Several of the specimens were also prepared by him. Others participating in the field work were: Mr. RICHARD RINKER (1950), Mr. JACK B. SENSINTAFFER (1951), and Dr. JOHN A. WHITE (1952). Dr. WHITE also worked in the laboratory as a volunteer. Museum assistants who contributed to building the collection during the indoor work were Mr. RANDALL WEEKS, and especially Mr. HAROLD A. DIETSCH.

Artists and the figures that they prepared are as follows: Mrs. LORNA CORDONNIER, figures 1-8, 39-40, 48-60, 72-73, 75-76, 78, 81; Mrs. SYLVIA E. BARR, figures

9-26, 29-30, 127, 132; Mrs. MARJORIE LAMB, figures 27-28, 31-38, 41-47, 61-71, 74, 77, 79-80, 82-126, 128-131.

Lastly, but not least, I thank Mr. ALBERT B. ROPER, rancher of West Plains, Colorado, for permission to excavate on his land, and Mr. CLYDE WARD and family, also of West Plains, for camping facilities for me and field parties from the University of Kansas at intervals over a period of years.

## RECOVERY METHODS

The quarry from which the faunule was obtained never became of large size, and was worked by man power alone. The larger mammalian specimens were recovered by orthodox methods. Part of the microfauna was found in the field, at the site, by careful breaking by hand of promising matrix into small pieces. Much of the residue of this operation was saved for later laboratory inspection, after a preliminary washing and drying eliminated the finest material. Less promising matrix frequently was screened as it was pick-axed from the quarry face for the occasional fragment of jaw or tooth it produced.

Especially rich-looking blocks were taken back to the laboratory in plaster jackets for later examination.

Laboratory search was carried out partly with the aid of a binocular microscope, but chiefly by a continuation of methods used in the field only under more favorable conditions of light and time.

Unfortunately, no satisfactory washing methods were ever developed for treating the matrix from Quarry A.

## OCCURRENCE OF FOSSILS

The faunule described here was obtained from a small excavation (approximately 75 cubic yards) in the Pawnee Creek Formation exposed in section 27, T. 11 N., R. 53 W., Logan County, Colorado. The fossils are contained in an impure (clay and silt), fine-grained sandstone. The more conspicuous particles are chiefly somewhat rounded quartz grains. Some biotite and other ferromagnesian minerals are present, together with a considerable quantity of feldspar—much of the latter decomposed. This sandstone is evidently fluviatile, and represents a channel fill. About 20 feet below the level of the quarry is a 15-foot cobble layer derived from nodular layers of the underlying White River Formation. It has not been ascertained whether the cobble layer and the beds containing the quarry represent one channel filling or several.

A definite bone bed or layer is not present. Although small lenslike concentrations of bone occur, the fossils are rather thinly scattered through several feet of sediment.

The quarry is characterized by an exceedingly high degree of fragmentation. Only two skulls (one oreodont and one rhinoceros) were obtained. In addition, two more specimens (peccary and beaver) consist of parts of skulls. Otherwise the specimens are jaws, isolated teeth, and post-cranial elements. Long bones are rarely complete. Articulated parts of the skeleton are absent except for the oreodont skull which had the mandible in contact with the cranium. Occasionally, however, parts are associated. For example, the peccary mentioned above is represented by a palate. It was in several pieces as originally found, but the individual parts were separated in the matrix by only a few inches. The beaver presents a situation similar to that of the peccary. Several other instances involve what are seemingly parts of the same individual found within a few inches or a few feet of each other. The most spectacular of such associations concerns the rhinoceros skull. Within a few feet of the skull were found a few limb bones which seemingly belong to the individual of the skull. Moreover, the skull is nearly toothless, and additional teeth (including lower cheek-teeth) apparently belonging to it were found some ten feet away. The entire specimen occupies, stratigraphically, some 3 or 4 feet of beds. Finally, there is present in the quarry a considerable quantity of what can only be termed scrap bone. This consists of more or less angular fragments, without terminations or character, derived from the shafts of the long bones of relatively large mammals.

The scrap bone tended to be concentrated in masses along with occasionally more complete specimens. Many of the jaws and teeth of small mammals were in these masses of fragments. The specimens of the larger mammals are clearly more fragmentary than those of the insectivores and rodents, and, for a reason not clear to me, the insectivores tend to be better preserved than the rodents or lagomorphs. Moreover, the large mammals almost invariably, unlike the smaller, fall into two groups as judged by the fossils; old individuals having well-worn dentitions, and young having unworn permanent cheek-teeth, and frequently deciduous teeth.

First examination of the specimens of Quarry A suggests shattered specimens unworn by transport. Delicate teeth and other parts are preserved in all original detail. Closer study, however, indicates a

patina of slight wear usually present, including wear on broken edges of bone.

Commonly, the fracture of bone is at an angle to the external surface, indicating, according to KUHNE (1956, p. 14), that organic matter was still present at the time fracturing occurred. [I am indebted to KUHNE's analysis of an entirely different kind of accumulation for several other points that I might otherwise have overlooked.]

Color of the bones and teeth varies from specimen to specimen. In some the teeth are nearly black and the bone a dark gray. In others, the bone is white and the teeth yellow or amber. Preservation in respect to water-wear is essentially the same in both, but the darker specimens suggest at times slightly greater wear. Occasionally, the darker specimens are found to be somewhat corroded, and the resulting small pits and channels filled with a claylike substance. At one stage in quarry excavation, it was considered possible that two sources of material were represented —one source consisting of reworked material from older beds. That the specimens are all essentially contemporaneous, however, is suggested by: (a) presence of specimens of intermediate color, and (b) presence of both extremes of color in the same specimen. For example, KU9279 has two cheek-teeth that are nearly black, and a third that is an amber color. Possibly on the whole, isolated cheek-teeth tend to be darker than those retained in jaws or pieces of bone.

No marks of the activities of rodents or mammalian carnivores were observed on any of the specimens.

What can be made of these data? First, there is an almost complete lack of articulation of elements or association of parts. The specimens, therefore, then must have undergone transportation after all connecting soft parts had disappeared. Transportation was generally not for any long distance, however, because of lack of wear on most specimens, and because of rare association of parts in some.

The first stage of transportation was by the flowing water of a stream. This stream was of fair size and had considerable transporting power for it moved fairly large masses of bone, and in the instance of the rhinoceros specimen previously mentioned, a fill stage resulted in deposition of several feet of fine sand. At one time I visualized a small, slow moving, meandering stream because of the fineness of grain of the sandstone and because of the areal distribution of the quarry and two additional concentrations of bone in a looplike patern reminding one of a meander. Nevertheless, the system of present day gullies is such as to be equally as likely to account for this pattern by removal of intervening outcrops, and perhaps essentially only one filling stage was involved from the base of the cobble zone to and including, at least, the sediments of Quarry A. Against this hypothesis, seemingly, is the lack of vertical grading of the sediments from coarse to fine. In any case, it seems necessary to invoke a rather large, swiftly-moving stream to account for the considerable amount of fragmentary and angular material. The nature of the fracturing suggests that some of it at least was accomplished while organic material was still present. The freshness of the bony surface, free from weathering or exfoliation, suggests that the bones did not remain for long on the surface of the ground.

I suspect that soft parts were destroyed chiefly after initial deposition in the stream fill, and that later erosion of the stream floor moved fossil material a short distance back-filling the scoured stream floor. Typical scour-and-fill bedding is, however, not to be observed. This event of scour-and-fill at a time when the bones were relatively brittle, and being denser than water not subject to floating, would account for the lack of association of parts, and the fragmentation that has occurred. Such a theory would not bar the occasional introduction of specimens more directly into the present site of accumulation.

Finally, I do not think that any of the specimens were transported far, and most of such transportation as did take place was by downstream action, and not by slope wash and soil creep. Thus, it is regarded as likely that most of the species recorded at Quarry A lived along the stream borders. Some kinds of small mammals possibly lived away from the riparian environment, and were transported thence by carnivorous birds or other predators.

## ECOLOGY OF QUARRY A

The presence of fishes, a large cryptobranchid salamander, and relatively common specimens of beavers support the thesis that the beds at Quarry A represent a channel fill. The preservation of the specimens, and some other features of the deposit, make it seem likely that most of the species represent a stream-border community. The large number of young and old individuals among the larger mammals (principally horse and deer) without an intermediate age group indicates a selective sampling of the population that could have, of course, several explanations. In the present case, I think it is that plant cover along the stream furnished protection for young and inexperienced ungulates and for old and infirm ones. The large number of ochotonid remains (*Oreolagus*

*nr. O. nebrascensis)* and the great scarcity of leporids —an unusual condition in the North American Tertiary—can also find an explanation in a stream-border environment, for a species of *Ochotona* (SHOTWELL, 1955, p. 335, 1956, p. 726) from the middle Pliocene of Oregon is a member of a stream-border community. The large number of shrews *(Heterosorex, Sorex)* and moles *(Mydecodon, Scalopoides, Proscalops?)* are also in agreement to the extent that some recent kinds are aquatic or are bank burrowers. TORDOFF (oral communication) states that the birds so far obtained could be inhabitants of a riparian environment.

The relatively great age of the site (early Miocene) prevents any direct proof of my environmental hypothesis. Instead, in the present state of our ignorance as to the ecological preference of most of the fossil mammals present, the "shoe is on the other foot," as it were, and we are in the position of hoping to ascertain these preferences by a study of the environment in which the remains are found. In the present instance, common animals in the thanatocoenose, if these can be determined, probably lived along the stream banks.

What were rare and what were common insectivores at Quarry A in regard to the living animals is uncertain. Possibly, some were rare but lived along the stream banks (with consequently more complete preservation); others were more common but lived farther away from the ultimate site of accumulation and are preserved as fragments. List No. 1 below is in order of abundance of specimens recovered, no attempt being made to record numbers of individuals. Even so, there is probably reasonably good correlation between numbers of specimens and numbers of individuals if comparisons are limited to the insectivores. The principal species in which abundance may be misleading are *Scalopoides isodens,* the only species in which postcranial elements (humeri) are counted, and *Proscalops* sp. cf. *P. secundus,* the only species rated as common, although known by isolated teeth alone. List No. 2 records percentages exclusive of humeri, and of the rare groups. List No. 3 includes those kinds represented by so few specimens that percentages of occurrence are not significant.

*Mammals from Quarry A*

*List No. 1*

(1) *Heterosorex roperi* (28)
(2) *Scalopoides isodens* (14 plus 11 humeri)
(3) *Plesiosorex coloradensis* (14)
(4) *Sorex vireti* (13)
(5) *Proscalops* sp. cf. *P. secundus* (11)
(6) *Sorex compressus* (7)
(7) *Mydecodon martini* (7)

*List No. 2*

| | *Percent* |
|---|---|
| (1) *Heterosorex roperi* | 30 |
| (2) *Plesiosorex coloradensis* | 15 |
| (3) *Scalopoides isodens* | 14 |
| (4) *Sorex vireti* | 14 |
| (5) *Proscalops* sp. cf. *P. secundus* | 12 |
| (6) *Sorex compressus* | 8 |
| (7) *Mydecodon martini* | 8 |
| Total | 101 |

*List No. 3*

(8) *Proscalops?* sp. (4)
(9) *Heterosorex? sp.* (3)
(10) *Plesiosorex?* sp. (2)
(11) *Metechinus* sp. cf. *M. marslandensis* (1)
(12) *Soricoid?* sp. indet. (1)
Total 116

If I were allowed subjective opinion, I would list the species in the following order of decreasing abundance at the quarry site: (1) *Heterosorex roperi* (2) *Scalopoides isodens* (3) *Sorex vireti* (4) and (5) *Sorex compressus* and *Mydecodon martini* (6) *Plesiosorex coloradensis* (7) *Proscalops* sp. cf. *P. secundus.*

Shrews make up most (50 percent) of the fauna with the aberrant *Heterosorex* clearly the most common. Moles are next in abundance (35 percent), and the metacodonts last (16 percent). The fauna is overwhelmingly soricoid.

A puzzling peculiarity of the insectivore fauna is the tendency for each genus to be represented by a large and a small species. An exception to this is the hedgehogs with but a single specimen, but otherwise it is true for all except *Mydecodon* and *Scalopoides.* Even here there is a size difference, but if my present conclusions are sustained, these two genera are not so closely related to each other as are the two species of *Plesiosorex, Heterosorex, Sorex,* or of *Proscalops.* Moreover, although the smaller is always the less common, the overall size range is considerable and this distribution does not seem to be due to the difficulty of finding smaller specimens. [In the rodents, it is prevailingly the opposite.] Reworking of significantly older beds seems hardly worth considering except possibly in connection with *Proscalops.*

The coexistence of four species of moles at Quarry A is difficult to accept. The fact that these are seemingly distributed among three genera, however, makes it a little easier to believe. The fragmentary and rare nature of one *(Proscalops?* sp.) suggests that this mole did not live in the immediate vicinity of the site

of deposition. The others (cf. *Proscalops, Scalopoides, Mydecodon*), represented by three different generic lines, may have had widely different habits. I think it probable that *Mydecodon* and *Scalopoides* had different levels of fossorial specialization, the latter being the more advanced in this regard. One of the three might have burrowed in the banks of the stream, being partly aquatic, and the third might have been largely either aquatic or bush-dwelling. This is sheer speculation, however, in the absence of post-cranial material save in one species (assigned here to *Scalopoides*). In this one, the animal was moderately specialized for fossorial life, but less so than are existing species of *Talpa* and *Scapanus*. Several European fossil localities have also produced remains of two or more kinds of moles so that Quarry A is not unique in this regard.

As with the insectivores, the relative frequency of occurrence of the various kinds of rodents in the deposit can not be ascertained with certainty. A simple order of abundance based on identifiable teeth and jaws follows. Percentages (totaling 99 percent) of the seven most common species also are given.

*Relative Abundance of Rodents at the Quarry A Site*

(1) *Monosaulax*, n. sp. (55=32 percent)
(2) *Mesogaulus paniensis* (36=21 percent)
(3) *Proheteromys galbreathi* (29=17 percent)
(4) *Plesiosminthus galbreathi* (17=10 percent)
(5) *Palaeoarctomys? bryanti* (15=9 percent)
(6-7) *Plesiosminthus clivosus* (8=5 percent)
*Pseudotheridomys hesperus* (8=5 percent)
(8) *Sciurus*, sp. A (7)
(9-10) *Mookomys* sp. cf. *M. formicorum* (5)
*Proheteromys* sp. cf. *P. magnus* (5)
(11-12) *Anchitheriomys?* sp. (3)
*Sciurus*, sp. B (3)
(13) *Florentiamys?* sp. (1)
Total, 192 specimens

The order of real abundance in the deposit is not necessarily given by the above figures. I judge, however, that *Monosaulax* is the most common rodent. *Mesogaulus* and *Proheteromys* are probably common, with possibly the latter the commoner of the two at the stream border itself. Of the others, *Plesiosminthus (Schaubeumys)* is probably represented by more individuals than the remaining ones. I would rate as common in the deposit any of the four named and forming with *Oreolagus, Heterosorex, Scalopoides,* and *Sorex* the chief microfaunal elements.

What is common at the stream border as opposed to what is common a short distance away from it is, of course, a major problem in the analysis of any quarry deposit. SHOTWELL (1955) has gone to some length to provide an answer, but I am not sure his elaborate analysis will prove too rewarding in practice. The theory back of his attempt seems sound, but a check case provided by counts of birds at McKittrick and Fossil Lake proved disappointing.

SHOTWELL thinks that it is possible to determine objectively which elements of a quarry fauna lived immediately around the site of deposition (what he calls the proximal community). His method is to identify every fragment in the matrix insofar as this is possible. The minimum number of individuals (based on duplication of the same element) for each species is determined. The total number of specimens of each species is counted and corrected to take into account variation in the number of taxonomically determinable elements in one kind of mammal as opposed to another. The corrected total number of specimens divided by the minimum number gives an average number of specimens per individual per species. This average number SHOTWELL takes as a measure of degree of completeness, and also as a measure of proximity to the depositional site. Arbitrarily, the proximal assemblage is then defined as that which shows more than the average number of elements per individual for the fauna as a whole. The idea of degree of completeness of preservation as a measure of proximity would seem obviously valid for mammalian assemblages except in the case of the exceptional animal rafted by stream from a relatively distant source. Nevertheless, I have felt that not much increase in accuracy of interpretation was really obtained, although increase in time and effort were. With some obvious exceptions, it has always seemed to me that little fossil material in a quarry site comes from a really distant source. The limited gathering ground and sampling errors of one kind or another would then result usually in little real distribution of the sort SHOTWELL suggests. As a test case, I investigated counts of specimens of fossil birds from Fossil Lake, Oregon (HOWARD, p. 141-195, 1946), and from McKittrick, California (DEMAY, p. 35-60, 1941). The use of birds rather than mammals should not make any difference in regard to degree of preservation as a test for proximity. I have not applied any correction factor for the number of specimens, for, generally, the same taxonomic groups of birds are included in both sites, and comparison is made between sites and not between species of the same site.

At McKittrick, birds are trapped essentially entire in the Pleistocene asphalt, but the figure of average

recovery is only 10 specimens per individual (based on determinable species, but not including passerines). At Fossil Lake, another Pleistocene locality, census of the avian fossils shows about six and a half specimens per individual. The Fossil Lake census was made on total collections of float material made for seven different institutions over a long period of years. There was no attempt made at complete recovery, and undoubtedly the fossils represent a variety of sublocalities. Two other asphalt accumulations yield figures comparable to that of McKittrick: the average from pit 10, Rancho La Brea, is between nine and ten, and from Carpinteria is ten and a half. These figures would suggest that the asphalt type of accumulation averages about ten specimens per estimated individual. The differential of three and a half specimens seems a rather narrow one in view of the extreme differences in methods of entombment and collecting. It does not leave much possible spread in working with more orthodox sites than tar pits.

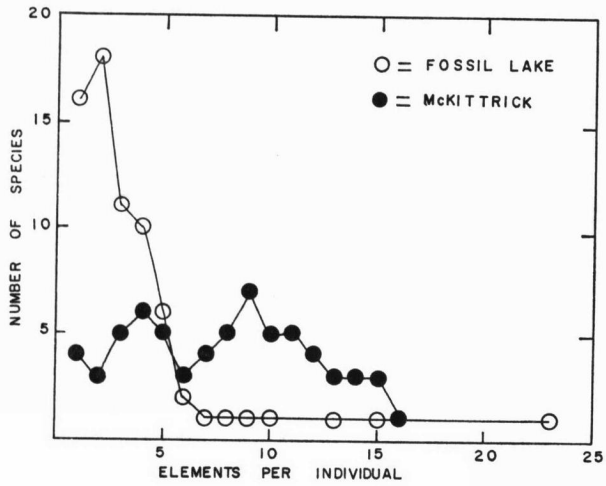



FIGURE 1. Graph of skeletal elements per individual plotted against number of species for McKittrick and Fossil Lake avian faunas.

Figure 1 shows two curves (all species are here used including, in these curves, those not formally named, and passerines as well as non-passerines), one for McKittrick and one for Fossil Lake, in which elements per individual is plotted against number of species. These curves do demonstrate the better preservation of the McKittrick fauna, but I think the most significant feature, unless there is a hidden flaw here in not using an adjusted figure for the number of elements per individual, is the lack of concentration of the McKittrick species at any particular value—a concentration to be expected with a trapping mechanism of entombment. Thus, four species are known only by single bones, and only five species have the mean value. The largest class (in the one unit intervals used) has only seven species in it out of a total of 66 species identified. Carpinteria has a similar distribution, although with a smaller number (37) of species. Four species are represented by single elements, and the largest number in any class is also four. In Figures 2 and 3 I have plotted in the same way material from McKay Reservoir and from Hemphill (Coffee Ranch) Quarry utilizing data (both corrected and uncorrected figures) given by Shotwell as examples of his method. The corrected figures here seem only to smooth out the curves without changing their fundamental shape. The McKay Reservoir curves (Fig. 2) are of the type seen in that for Fossil Lake with a concentration of species represented by few elements per individual. The Coffee Ranch curves (Fig. 3) are much more nearly like those of McKittrick and Carpinteria with no concentration of species, although, in the former, the distribution is somewhat irregular, perhaps because of the small number of species included. I suggest that where all species are living approximately equally far from the site of deposition that a curve of the McKittrick type is produced; that where some important part of the faunule is farther away, the rare scattered elements thus added to the depositional site modifies the McKittrick-type distribution to produce the Fossil Lake and McKay types of curves; and that a low number of elements per individual in itself does not indicate distance from the depositional site. If this is so, then we can only say that certain species were perhaps outside the proximal community, others almost certainly in it.

It seems to me also that it remains to be demonstrated how much more accurate the method proposed by SHOTWELL is than is one using percentage calculations derived directly from number of specimens, with perhaps some subjective adjustment for other considerations. In any case, the Quarry A material does not permit of more refined treatment at present, for the bulk of the postcranial material has not been sorted, and much of it would be nearly impossible to assign except in a tentative way. Moreover, the depositional history, if it is as I have proposed, would produce a low number of elements per individual regardless of proximity.

In a later study by SHOTWELL (1958), methods are modified slightly and extended to collections not covered in the 1955 paper. My own comments were written before the publication of the later publication, but it does not seem necessary to alter them.

I speculate that *Monosaulax, Plesiosminthus (Schaubeumys),* and probably *Proheteromys* were abundant rodents in the quarry vicinity during deposition. *Mesogaulus* may or may not be in this category. The frequency of occurrence may be the result of large size, and possibly extraordinary abundance some distance away from the stream. The widespread occurrence of mylagaulid remains in late Miocene and Pliocene faunules suggests that the

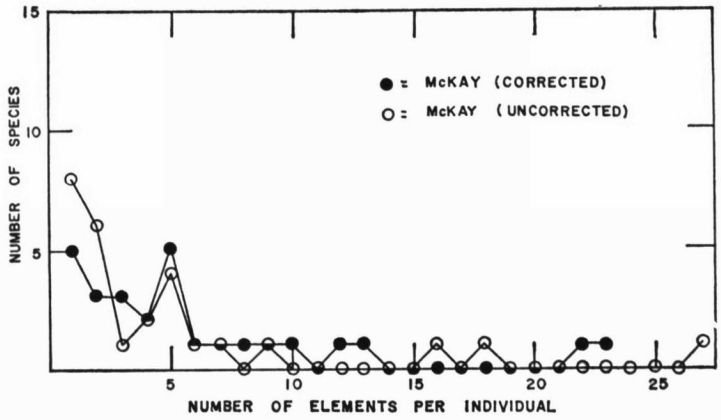



FIGURE 2. Graph of skeletal elements per individual plotted against number of species for McKay mammalian fauna. Corrected curve is adjusted for variation in taxonomically determinable elements from one species to another.

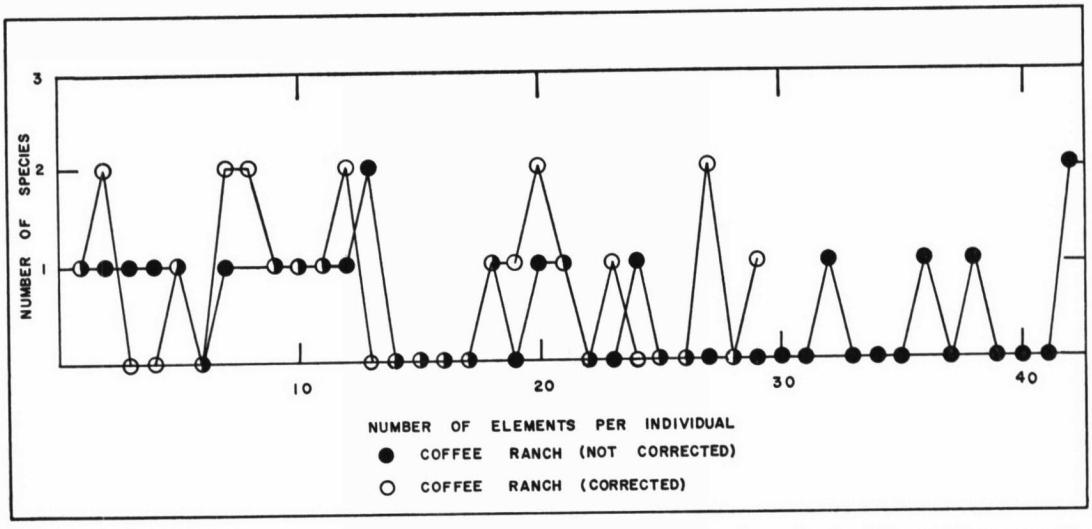



FIGURE 3. Graph of skeletal elements per individual plotted against number of species for Hemphill mammalian fauna. Corrected curve is adjusted for variation in taxonomically determinable elements from one species to another.

distribution of these animals was not controlled by small changes in the environmental factors. Nevertheless, the large number of "fresh" teeth in this deposit suggests that the stream in which the sediments were deposited was an effective factor in their relative abundance, if only as a hazard factor to the young. If *Proheteromys* is merely a structural stage in the evolution of heteromyids or heteromyines, its "presence" has no significance. *Schaubeumys* has *Sicista* as its closest modern relative. Species of the extant genus are tree-climbing and inhabitants of wet, woody places. They would be at home in riparian vegetation. *Monosaulax* is seemingly ancestral to *Dipoides*. This latter genus is probably amphibious, and *Monosaulax* could have lived in the stream in which the Quarry A sediments were deposited. Several of the rarer species also are possible inhabitants of the supposed riparian niche. *Plesiosminthus* is closely related to *Schaubeumys,* and among the sciurids, both *Sciurus* and the chipmunklike *Palaeoarctomys? bryanti* suggest the presence of trees or other arboraceous vegetation. How difficult estimations of environment really are can be seen when comparison of the Quarry A fauna is made with a similar one of later (Sheep Creek) age from Wyoming, the Split Rock microfauna.

*Comparison of Quarry A Fossils and Split Rock*

| QUARRY A | SPLIT ROCK[a] |
|---|---|
| Insectivores, abundant | *Metechinus marslandensis* |
| *Oreolagus* | Talpid sp. |
| *Hypolagus?* sp. | *Oreolagus* |
| *Mesogaulus paniensis* | Leporid |
| *Sciurus* | *Mesogaulus novellus* |
| *Palaeoarctomys?* sp. (*Tamias*-like form) | *Protospermophilus* |
| | *Tamias?* |
| Cf. *Mookomys* | *Perognathus* |
| *Proheteromys* sp. | *Peridiomys* |
| *?P.* sp. cf. *P. magnus* | *Gregorymys* |
| Entoptychinae | *Pleurolicus?* |
| No Geomyinae | *Dikkomys* |
| *Schaubeumys, Plesiosminthus* | *P. (Schaubeumys) sabrae* |
| Castorids | No Castorids |
| Eomyids | No Eomyids |

The chief differences among the rodents of the two assemblages are: (a) lack of beavers at Split Rock, and (b) geomyids rare at Quarry A. This suggests that one was stream-border location and the other something else. If so, such species as the fossil zapodids and sciurids are not riparian, but their presence might still indicate arboraceous cover. A discrepancy here is that both localities yield ochotonid remains that, so far as Quarry A is concerned, I have interpreted to indicate some special stream-border condition because of the prevailing dominance of leporids in most other fossil deposits. If the presence of *Monosaulax* was controlled not only by the existence of streams or standing water, but also by more restrictive condition within this particular niche, the difficulty would be largely overcome. Other accumulations of a similar nature are needed, however, before we can speculate further on this.

As among the insectivores, large and small species of more or less related kinds of rodents tend to be present. Unlike the insectivores, however, the paired species belong to different, although related, genera rather than to the same genus. Perhaps this difference is largely one of differing taxonomic scales in the two orders. It may also indicate that among rodents more than insectivores, coexistence of related species depends on several other factors in addition to size. Also, unlike the insectivores of Quarry A, among the rodents it is the larger of the two species, in all cases save one, which is relatively rare. These pairs are: *Palaeoarctomys?* and *Sciurus; Monosaulax* and *Anchitheriomys?; Proheteromys galbreathi* and *Proheteromys* sp. cf. *P. magnus; Plesiosminthus* and *Schaubeumys.* Only *Mesogaulus* and *Pseudotheridomys* are represented by completely isolated species.

One major group of rodents is absent from the fauna, the Cricetidae. This absence is made striking by the abundance of *Eumys*-like species in the underlying White River Formation. However, members of this family are rare in the Arikareean (they are all pre-Marsland), and ?absent in Hemingfordian collections. It is not until late Barstovian time that they reappear as common elements in the known American fauna. Their widespread absence, then, indicates that their absence at Quarry A cannot be attributed to local environmental factors. Their ecologic place seems to have been occupied by various heteromyids, and possibly even by unspecialized zapodids. Among geomyids, the entoptychines are recorded only by several isolated teeth. They are known by two rather good specimens in beds around the quarry, and, of course, are common fossils at many North American localities in slightly older beds. The entoptychines, fossorial or otherwise, may have preferred areas away from stream borders, although as previously stated, this view is not without weaknesses.

[a]Fauna now being studied by BLACK, and BLACK & WOOD, generic list by courtesy of C. C. BLACK.

## GEOLOGIC AGE AND CORRELATION OF THE FAUNA

The microfauna of Quarry A is part of a larger fauna termed the Martin Canyon local fauna by GALBREATH (1953, p. 32), and regarded as the lowest faunal level occurring in the Pawnee Creek Formation.[1] This part of the Pawnee Creek is clearly intermediate in age between those of the White River and those of the Mascallian and later faunas. In its rodent fauna it bears a decided resemblance to a known Sheep Creek microfauna (Split Rock) but it seems to be recognizably distinct from that. In part or in its entirety, the Martin Canyon is surely the equivalent of the old "upper Harrison" of Nebraska, now generally termed the Marsland (SCHULTZ, 1938). The position of the Quarry A faunule relative to successive

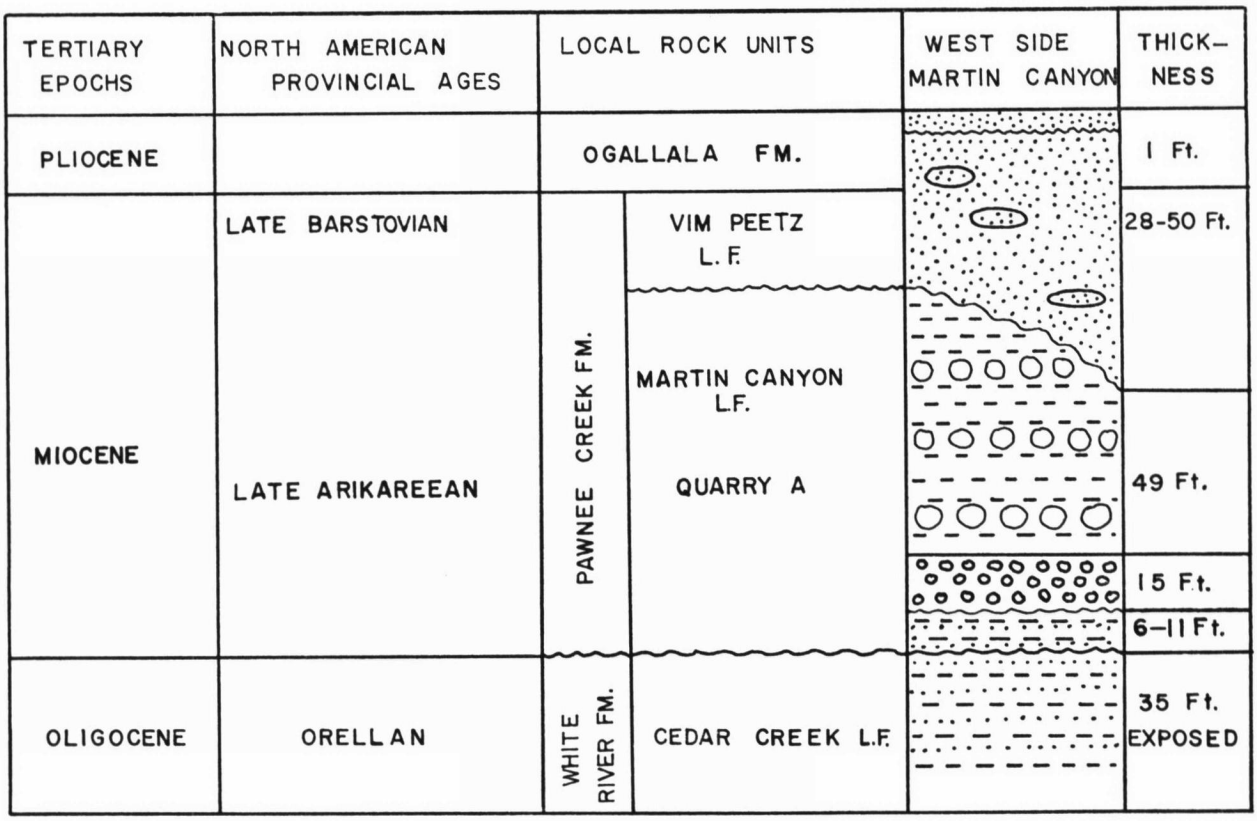



FIGURE 4. Correlation of Quarry A with other local rock units, and its fauna with standard North American provincial ages.

[1] It is doubtful whether the beds containing the Martin Canyon local fauna should really be assigned to the Pawnee Creek Formation. In Martin Canyon itself, beds immediately overlying those containing the Martin Canyon local fauna are of much later age (Barstovian). Nowhere, so far as now known, are beds of Sheep Creek age (restricted) found in northeastern Colorado. Finally, the type fauna of the Pawnee Creek (Eubanks local fauna) is considerably later than the Martin Canyon. The name Martin Canyon Formation might be used, but has been previously rejected by GALBREATH for good reason (1953, p. 20). The name Marsland might also be introduced from the Nebraskan sequence. It is true, however, as GALBREATH indicated, that beds containing the Eubanks and Kennesaw faunas are not readily distinguished from those containing the Martin Canyon assemblage except by fossil content. Perhaps, then, it is still a convenient device to assign the Martin Canyon beds to the Pawnee Creek Formation.

levels in the Nebraskan Marsland may be subject to some doubt, but is either middle or upper. The lowest levels of the Martin Canyon contain the old American Museum *Merycochoerus* quarry regarded by SCHULTZ & FALKENBACH (1940, p. 284) as somewhat later than the lowest Marsland, as indicated by the presence of *M. (P.) magnus,* and the beds containing this quarry are locally separated by an unconformity from those of Quarry A. Further, *Merychyus elegans* is identified by SCHULTZ & FALKENBACH (1944, p. 192) as occurring in the Martin Canyon section and is classified as

upper Marsland. This species almost certainly came from above the American Museum quarry level. Specimens of *Merychyus* are, in fact, rather common at the level of Quarry A. However, the Quarry A beds are not so high as to be later than the "upper Harrison," if COOK & GREGORY (1941, p. 549) are correct in maintaining that the Marsland of SCHULTZ includes some distinctly later beds. In any case, the faunule of Quarry A is accurately enough placed to be of great value if it could be correlated at all precisely with those of Europe.

Figure 4 relates Quarry A to the standard North American sequence as well as to the section at Martin Canyon. I have placed the Quarry A and Marsland levels in the late Arikareean, rather than the early Hemingfordian, because the fauna in Martin Canyon is clearly an advanced phase of the underlying Harrison. It contains a number of genera and groups regarded as distinctive of the Arikareean as defined by WOOD *et. al.* (1941, p. 12). The following "index fossils" of the Arikareean are present in the Martin Canyon local fauna and Marsland (Nebraska) equivalents: *Diceratherium, Entoptychinae, Oxydactylus, Stenomylus,* and *Syndyoceras. Parahippus* is the most advanced horse.

A number of workers have attempted to correlate Miocene sequences in North America with those in Europe. Whatever the merit of any individual attempt may be, there has not been unanimity of opinion, to say the least. The question, then, as to the position of the Quarry A microfauna (and the Marsland) relative to a standard European sequence is difficult to answer.

First, the more general attempts at correlation may be considered. For this purpose Figure 5 compares charts by (1) the WOOD Committee (1941); (2) STIRTON (1951); and (3) SCHULTZ & STOUT, and STOUT (various sources). The Aquitanian is regarded by WOOD and STIRTON as more or less the equivalent of the Arikareean but as the equivalent of the Whitneyan by SCHULTZ & STOUT (1955, p. 46). The Hemingfordian is regarded as nearly the equivalent in scope of the Burdigalian by STIRTON, but only in part by WOOD (below the Sheep Creek local fauna), and probably not at all by SCHULTZ & STOUT. The well-known middle and late Vindobonian faunas of Europe (Sansan, La Grive St. Alban, Simorre) would be regarded as Sheep Creek *(s.s.)* by WOOD (upper Hemingfordian), as Mascall—Niobrara River (Barstovian) by STIRTON, and as ?Marsland, (principally Sheep Creek) by SCHULTZ & STOUT. The Sarmatian is regarded as Barstovian by WOOD, as early Barstovian (pre-Valentinian) by STOUT (written communication), but as largely Clarendonian by STIRTON. Standard correlations based on marine invertebrates would place most of the Clarendonian in the Miocene (WEAVER *et. al.,* 1944), and some authorities would put part of the Arikareean in the Oligocene.

These differences in correlation arise in two ways: (a) differences of opinion as to the correlation of

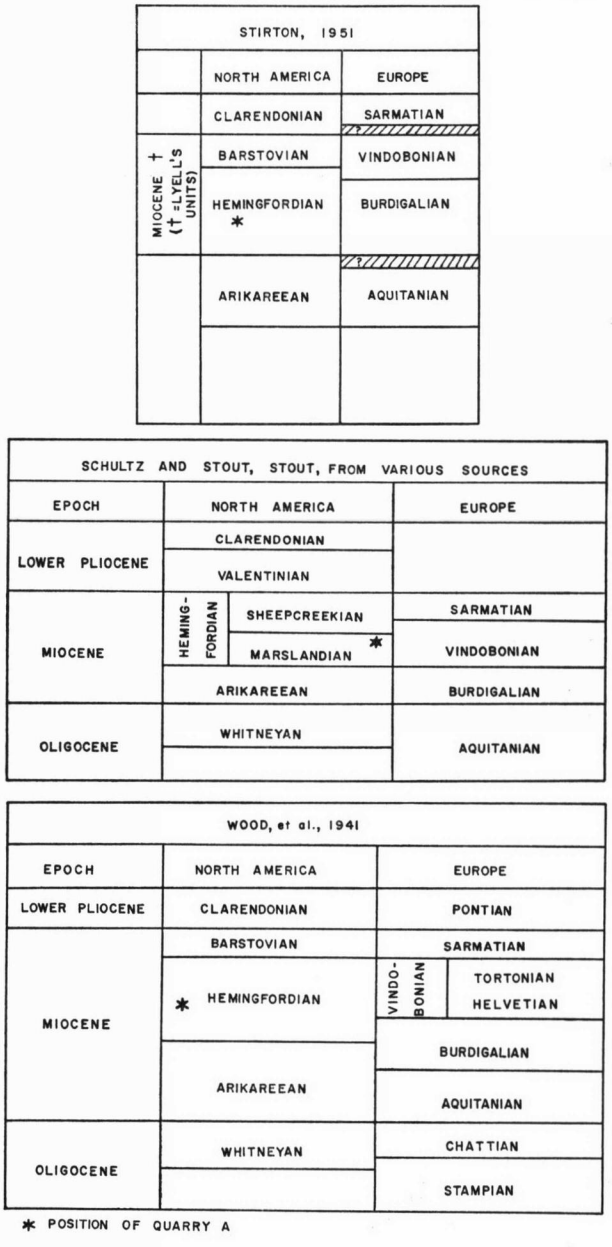



FIGURE 5. Some proposed correlations of the North American provincial ages with European standards.

individual faunas on the two continents (e.g., correlatives of the Estrepouy or the Harrison) and (b) differences in the application of the European stage names, (e.g., Sarmatian). The Sarmatian of SCHULTZ & STOUT is something quite distinct from that of STIRTON. That of the former authors would contain no hypsodont horses, but that of the latter would contain typical *Hipparion*. The artificial differences of type (b) can be eliminated by comparing largely on a faunal basis as PILGRIM (1940, p. 10-11) essentially has done, although this procedure has the defect of claiming more accuracy than the author intends. Differences in correlation can, of course, be eliminated also by refinement of work to the point where all authors agree as to what each of the standard stage names covers: at present this highly desirable state of affairs is far from realized.[2]

In my own correlation, I have eliminated from consideration the Sarmatian and the Chattian. It seems reasonably certain that the sequence of mammalian faunas assigned to the Stampian and Aquitanian cover the time occupied by the Chattian. The Chattian may be a facies of the late Stampian (BRINKMANN, 1954, table opp. p. 254) or of the Aquitanian (DURHAM, 1944, p. 250), or spread out over both. Likewise the Sarmatian seems to me to be not distinct in practice. Faunas assigned to its lower part seem closely related to those assigned to the late Vindobonian of some areas, and its upper part carries *Hipparion* which is used to indicate the Pontian in most localities (GLAESSNER, 1953; J. H. MAXSON, personal communication). The fact that the Sarmatian overlies the Vindobonian in the type area of the Vienna Basin (GLAESSNER, 1953, p. 65) is small practical comfort to the vertebrate paleontologist working in areas farther west. M. CRUSAFONT PAIRO (1951, p. 36, fig. 2; p. 38, fig. 3) regards the Sarmatian as a phase of the late Vindobonian, as did GIGNOUX (1950) on other grounds, on the basis of the section in Spain. A fauna having primitive *Hipparion* in the Spanish sequence may correspond approximately to that of St. Gaudens, Oeningen, and Monte Bamboli, which have been variously called late Vindobonian and early Sarmatian (COLBERT, 1942, p. 1465), but this is only speculation on my part. This fauna is said by CRUSAFONT to follow immediately on an equivalent to La Grive St. Alban, and obviously contains many comparable elements. STIRTON's correlation, given above, has been greatly influenced by CRUSAFONT's work in Spain. COLBERT (1942, p. 1466) has suggested also that perhaps no Sarmatian mammalian faunas (in a strict sense) are known.

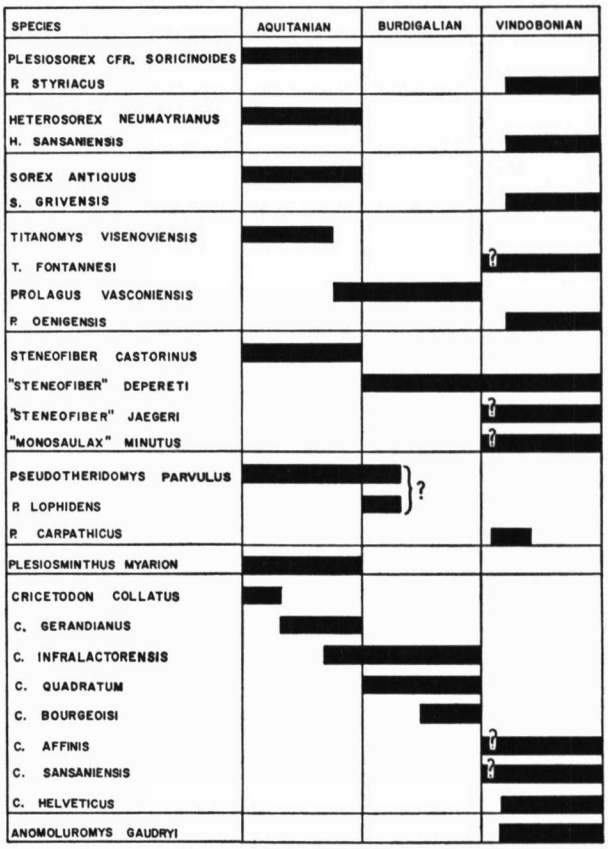



FIGURE 6. Stratigraphic ranges of some European mammals

Some other difficulties in the way of correlating the Quarry A assemblage may be mentioned before turning to this faunule. The position of any one faunule relative to others of North America is agreed upon almost without dispute save in one important exception, the John Day. Most authorities have regarded the middle and upper John Day as pre-Harrison and immediately post-White River. SCHULTZ & FALKENBACH (1949, p. 83) regard it as Harrison in age. Unfortunately, it is the John Day that figures largely in many attempts to correlate the earlier Miocene of Europe with that of North America. I

[2] The European stages are based and defined on physical records with definite type localities which may, probably frequently do, overlap each other as the names are used away from the type areas. The American stages are primarily defined on organic records (in practice if not in theory), and defined so as to be mutually exclusive. This difference in scope becomes the source of error and confusion when reduced to chart form.

regard the John Day (middle and upper) as a near-equivalent of the typical Aquitanian, as long supposed, but more recently disputed by SCHULTZ & STOUT. The microfauna in the post-Aquitanian-pre-Sansan interval is rather poorly known in Europe (Fig. 6). There is a faint suggestion that the Aquitanian species extend into the Burdigalian more frequently than do Vindobonian species, but the earliest Vindobonian is also poorly known. Lastly, although faunules as the Mascall and lower Snake Creek are almost surely Vindobonian, a difficulty of correlation lies in the fact that the relation of the Sansan to the La Grive St. Alban is not altogether clear. Earlier authors have usually thought of the Sansan as older, but many species are common to the two faunas, and some recent authors have treated these as essentially contemporaneous (CRUSAFONT PAIRO, 1951, p. 39; also suggestion along these lines by COLBERT, 1942).

The microfauna at Quarry A rather consistently favors a post-Aquitanian date. Only in *Plesiosminthus* does a Quarry A species seem somewhat more primitive than the known Aquitanian ones. This indication of post-Aquitanian age is not surprising as all opinions previously expressed would give a post-Aquitanian date to the Marsland. At the younger end of the time scale, there is evidence that the microfauna of Quarry A is older than that represented by Sansan and La Grive. Thus this microfauna seems no younger than early Vindobonian. This also is in agreement with previous opinions. Do the rodents and insectivores help to narrow the placement still more? The resemblance of the rodents to the Split Rock local fauna of Sheep Creek age is sufficient, in spite of a difference in age, as to cause no surprise that correlation with similar European faunas is difficult. They do, however, I think, suggest to a certain extent Burdigalian as the most likely correlation of the Marslandian, and possibly even early Burdigalian. As supplement to Figure 5, I would correlate the faunas and stratigraphic units as shown in Figure 7.

| EUROPE | | EUROPEAN FAUNAS | NORTH AMERICA | AGES | |
|---|---|---|---|---|---|
| VINDOBONIAN | "SARMATIAN" | (10) OENINGEN, ST. GAUDENS, MT. BAMBOLI, CAN POSIC | ? TONOPAH, NIOBRARA RIVER | BARSTOVIAN | |
| | "TORTONIAN" | (9) LA GRIVE-ST. ALBAN, SIMORRE, ST. QUIRZE (FERROCARRIL) | LOWER SNAKE CREEK | HEMINGFORDIAN | MASCALLIAN |
| | | (8) SANSAN | MASCALL, VIRGIN VALLEY, | | |
| | "HELVETIAN" | (7) CASTELNAU L'ARBIEU | SHEEP CREEK | | SHEEPCREEKIAN |
| BURDIGALIAN | | (6) ROMIEU<br>(5) ESTREPOUY, ORLEANAIS | ? COOK'S MARSLAND | | |
| AQUITANIAN | | *(4) LAUGUAC, FRANKFURT | MARSLAND<br>HARRISON<br>MONROE CREEK | ARIKAREEAN | MARSLANDIAN |
| | | (3) ST. GÉRAND-LE-PUY, CHAVROCHES, ALLIER | GERING, JOHN DAY | | HARRISONIAN |
| | | (2) PAULHIAC | | | |
| UPPER STAMPIAN | | (1) PEUBLANC, BRANNSAT | WHITNEY, LAS POSAS | WHITNEYAN | |

*AQUITANIAN SEQUENCE FROM HÜRZELER, 1946

FIGURE 7. Suggested stratigraphic correlation of some North American and European fossil faunas.

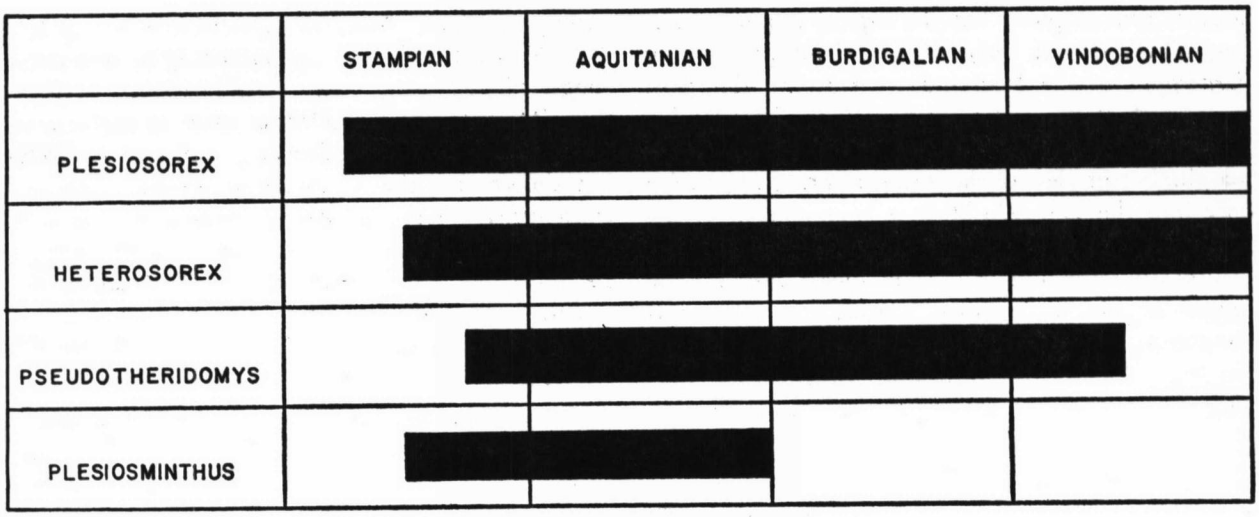



FIGURE 8. Stratigraphic ranges in Europe of mammalian genera also present at Quarry A.

Certain species of the microfauna of Quarry A contribute evidence as to its age relative to European faunas as follows:

(1) *Plesiosorex*. The American species may be slightly more advanced over the Aquitanian, *P. cfr. soricinoides*; it seems more primitive than the late Vindobonian (and Sarmatian) *P. styriacus*.

(2) *Heterosorex*. The American species is probably less advanced than the Tortonian *H. sansaniensis*; but except in larger size, it is difficult to demonstrate its advance over the Aquitanian *H. neumayrianus*.

(3) *Sorex*. No species of "Sorex" is recorded earlier than Aquitanian. The Quarry A species may favor a post-Aquitanian date, but evidence is weak.

(4) *Oreolagus*. In stage of evolution, *O. nebrascensis* is advanced over the Aquitanian species of lagomorphs, but it is less advanced than some Burdigalian species.

(5) *Palaeoarctomys?*. The American species is possibly more progressive than Aquitanian, and even the early Burdigalian species of squirrels, but it is less advanced than those of the Tortonian.

(6) *Anchitheriomys?*. The species is more advanced in size (larger) than Aquitanian beavers, but less advanced in hypsodonty than the Burdigalian species (*"S." depereti*). *Anchitheromys (s.s.)* is not known earlier than upper Vindobonian, but the Quarry A species is distinctly more primitive, being in essence a large variant of the Aquitanian *Steneofiber castorinus*.

(7) *Monosaulax*. The Quarry A species is less hypsodont although agreeing with Vindobonian *"Monosaulax"* in size. [The European *"Monosaulax"* is not known before the Vindobonian, but may not be closely related.]

(8) *Pseudotheridomys*. The American species seems less advanced than the early Vindobonian, *P. carpathicus*. It is essentially at the level of the Aquitanian and early Burdigalian *P. parvulus*, but it might be slightly more advanced.

(9) *Plesiosminthus*. In degree of compression of the lophs of the upper cheek-teeth, the American species does not seem so advanced as *P. myarion* of the late Aquitanian. No post-Aquitanian European records are known.

The four extinct genera of Europe with records also at Quarry A have considerable stratigraphic range so that these by themselves are of small value for correlation (Fig. 8).

The evidence to be obtained from the larger mammals present in the Marsland and Quarry A faunas is not great. The presence of numerous cervids, but no antilocaprids is paralleled in Europe by the Burdigalian faunas. The first antilocaprid in North America is seemingly Sheep Creek, and the first bovid in Europe (contrary to SIMPSON, 1945) seems to be *Eotragaceros* of the Sansan (LAVOCAT, 1955, p. 688). This fragile line of evidence suggests a late Burdigalian age for the Marsland. The *Diceratherium* of the Marsland is certainly different from *D. asphaltense* and *D. pleuroceros* of the Aquitanian (SCHAUB & HÜRZELER, 1948, p. 361-365). However, these Euro-

pean records suggest that the typical Aquitanian is post-Whitneyan, if only slightly. The presence of *Parahippus* in the Marsland whereas the European horse is *Anchitherium* suggests that the Marsland is later than the early Burdigalian by a considerable margin, but in view of the introduction of *Hipparion* only into the Old World at a later date, it is not necessary to insist that the Burdigalian introduction of *Anchitherium* was before the appearance of *Parahippus* in North America. Further, if SCHULTZ & FALKENBACH are right in their correlation of the John Day and Harrison (a correlation which seems somewhat dubious to me), *Parahippus* may have been restricted to the Plains area at first.

Aside from the Marsland genera, there are of course others, both earlier and later, which have been used in intercontinental correlation, but not with any marked success. Several of the more recent entries into the field are discussed below, but I will not repeat old arguments based on *Anchitherium, Moropus, Hemicyon, Ursavus,* and the like.

VANDERHOOF (1941) has written a note concerning the discovery of a sea-cow in Tertiary sediments of California, which he states is close to or possibly specifically identical with *"Metaxytherium" petersi* from the Vindobonian of the Vienna Basin. He further states that *M. cuvieri* is an ancestral species from the Helvetian, and hence the Californian species may be Tortonian. So far as I can determine, the Californian species is from the Santa Margarita sands of Cierbo or Neroly age. This suggests an early Clarendonian age, one seemingly too young for the Tortonian. It is a difficult correlation to accept if reliance is placed on *Hipparion,* for the first appearance of the hypsodont horses is pre-Neroly, and probably Briones. VANDERHOOF's sea-cow would seem to be a contemporary of these horses, and possibly is later than their first appearance. Of course, *Hipparion* might have reached Europe considerably after its appearance in North America. I regard, however, the first appearance of *Hipparion* in eastern Europe as rather near to the time when the *Hipparion* group (as fully hypsodont forms) evolved in North America; hence, the "upper Sarmatian" (Chersonian), and Can Ponsic (NW de Can Mata) of Spain would be approximately equivalent to the earliest Clarendonian. A possible explanation of the conflicting evidence offered by the Californian *"Metaxytherium"* is that *Metaxytherium* (properly *Halianassa* according to SIMPSON, 1945) is difficult to distinguish from the Pliocene *Felsinotherium* (SIMPSON, 1932, p. 451), and perhaps the Santa Margarita species is of this genus. That VANDERHOOF's determination may be in error is suggested also by another consideration. He states that *"M. petersi"* of California may be ancestral to Stellar's sea-cow *(Hydrodamalia).* SICKENBURG (1928) has shown that the Viennese M. *petersi* is distinct from other species of *Metaxytherium* to a marked degree, and he has named *petersi* as the unique species of the genus *Thalattosiren.* Of *Thalattosiren,* SIMPSON (1932, p. 479) remarks that it could not be ancestral to any living sirenian. Hence, this valuable record in California needs further clarification.[3]

*Elomeryx* is known only from the Whitneyan of North America, and the early Aquitanian of Europe. According to MACDONALD (1956), the line is American, *Elomeryx* having descended from *Aepinacodon.* This then would mean that *Elomeryx minor* of the early Aquitanian could be no older than Whitneyan, and certainly not a great deal younger either, for MACDONALD (1956, p. 639) thinks that *Arretotherium* (Arikareean) is derived from *Elomeryx,* and even suggests (text fig. 1) that *Kukusepasutanka* (Harrison equivalent) is derived from the European *Elomeryx.* This seemingly, then, is an important genus in correlation. MACDONALD also records, tentatively, the presence of *Elomeryx* in the Kew Quarry of the Sespe. Although the Kew Quarry is currently regarded as Whitneyan, the Carnivora particularly have such a striking resemblance to those of the John Day (STOCK, 1933a, p. 41) as to suggest that the John Day fauna follows immediately after the Whitney in time as an equivalent of the Gering rather than of the Harrison. The Kew Quarry horse (*Miohippus* sp.), also, suggests a relationship to the John Day rather than to the Whitney (STOCK, 1933, p. 26). It is perhaps significant stratigraphically rather than facially that *Miohippus,* but not *Parahippus* is present in the Gering, Kew Quarry, and John Day faunules.

A species of *Allomys* agreeing closely with *A. cavatus* of the John Day, has been recorded by PIVETEAU (1934) from the Quercy Phosphorites. He has noted also that *Allomys* and *Sciurodon* probably are synonyms. Granted that the two genera are remarkably alike, the phosphorites are not known to range upward beyond the earlier Stampian (Rupelian) and the John Day is hardly as old. Nevertheless, this

[3] Partial clarification is in fact obtained by the appearance of R. H. REINHART's study ("A Review of the Sirenia and Desmostylia," Univ. Calif. Publ., Geol. Sciences, 36, no. 1, 1959) long after the above was written. The stratigraphic implications of VANDERHOOF's specimen, however, remain obscure.

record is another instance of resemblance of a John Day genus to Aquitanian or earlier European genera.

A fourth genus, *Haplocyon,* may be mentioned, although previously figuring in a discussion by PILGRIM (1940, p. 16). *Haplocyon* is known by two European species, *H. crucians* (St. Girand le Puy, middle and typical Aquitanian) and *H. dombrowskii* (La Miloque, lower upper Stampian). VIRET (1929, p. 126-28) has sugested that *Haplocyon* is synonymous with *Temnocyon* (Whitneyan to Harrisonian of North America). HELBING (1928) had previously pointed out the resemblance of *Haplocyon* and *Temnocyon*. The Kew Quarry has produced *Temnocyon cf. altigenus* (*T. altigenus* is a John Day species). So far as this admittedly slight evidence is concerned, the upper Stampian could be correlated with the Whitneyan, and the Aquitanian with the John Day.

Frequently ignored by American vertebrate paleontologists in discussions of correlation with Europe is the evidence furnished by marine metazoan invertebrates. Admittedly less satisfactory than mammals in many ways, the marine invertebrates have the one advantage of furnishing a facies comparable to that of the standard European sections. Almost all workers with marine mega-invertebrates (COOKE *et al.,* 1943; WEAVER *et al.,* 1944) would place the marine equivalent of the North Coalinga local fauna —this local fauna is from a deltaic deposit interculated with a marine section—in the Vindobonian, perhaps favoring a lower Vindobonian (Helvetian) age. The North Coalinga local fauna would then be roughly equivalent to the Sansan, a not unreasonable correlation on the basis of mammals alone. Miocene correlations based on Foraminifera, however, place this California faunule as mid-Burdigalian. Hence, the marine organisms do not furnish us with an unequivocal correlation. Nevertheless, the marine record is of some interest in connection with a mammalian faunule, the Tick Canyon local fauna, of possible contemporaneity with Quarry A. The Tick Canyon of southern California is regarded as of Marslandian age by JAHNS (1940, p. 169), its describer. SCHULTZ & FALKENBACH (1947, p. 188) have claimed it to be Harrisonian. JAHNS (p. 177), as well as DOUGHERTY (1940, p. 129) have regarded the Tick Canyon as approximately upper Relizian on the Californian marine scale. The upper Relizian would be considered Aquitanian by foraminiferal workers, and as upper Burdigalian by those studying metazoan invertebrates.

Obviously considerable differences of opinion exist in regard to long range Miocene correlations, and any particular one, including my Figure 7, must be regarded as tentative. Moreover, I do not wish to suggest in mine that the Sansan is, in fact, the equivalent of the North Coalinga faunule. It is, however, more misleading in the present case to use stage names with their varying content than the materials of long-range correlations themselves, even if, as in the present case, it may lead to inferring a precision not present. There is nothing especially original in my correlation, but it manages, as a working hypothesis, to be consistent with most of the evidence, and to be supported, positively, by a considerable number of data.

## DESCRIPTION AND DISCUSSION OF FOSSIL VERTEBRATES

### LOWER VERTEBRATES

A considerable number of fragmentary specimens of lower vertebrates have been recovered at Quarry A, but work on them is still in a preliminary stage. Some fish remains are present. Most interesting specimens, perhaps, of the cold-blooded types, are some vertebrae and other parts of a large salamander. They are possibly of the *Cryptobranchus japonicus* type, although there is no evidence that the species grew to as large a size as the large individuals of this species. Of reptiles, both testudinates and lizards are to be recorded. Several bones of birds have been found, and these are now being studied by Dr. HARRISON B. TORDOFF. The presence of fishes and the large cryptobranchid salamander furnishes evidence in support of the interpretation of the deposit at Quarry A as a channel fill.

### HIGHER VERTEBRATES
### Class MAMMALIA

The larger mammals will form a separate study. A preliminary faunal list is given below.

*Larger Mammals of the Martin Canyon Fauna*

| | |
|---|---|
| Carnivora | Artiodactyla |
| *Cynodesmus?* | *Hesperhys* |
| Amphicyonine sp. | *Merycochoerus proprius magnus* |
| Perissodactyla | *Merychyus* |
| *Parahippus pawniensis* | *Oxydactylus* |
| Dicerathere? rhinoceros | *Barbouromeryx* |

Remains of carnivores are extremely scanty. Of the ungulates, the common kinds are of horse and deer, mostly in a juvenile or aged condition. The larger mammals are noteworthy in their scarcity of mature or nearly mature individuals.

*Smaller Mammals of the Martin Canyon Fauna*

Order Insectivora
- Family Erinaceidae
  - *Metechinus* sp., cf. *M. marslandensis* Meade
- Family Metacodontidae
  - *Plesiosorex coloradensis*, n. sp.
  - *Plesiosorex?* sp.
- Family Soricidae
  - Subfamily Heterosoricinae
    - *Heterosorex roperi*, n. sp.
    - *Heterosorex?* sp.
  - Subfamily Soricinae
    - *Sorex vireti*, n. sp.
    - *Sorex compressus*, n. sp.
- Family Talpidae
  - Subfamily Scalopinae
    - *Mydecodon martini*, n. gen., n. sp.
    - *Scalopoides isodens*, n. gen., n. sp.
    - *Proscalops* sp. cf. *P. secundus* Matthew
    - *Proscalops?* sp.
  - Soricoid?, sp. idet.

Order Lagomorpha
- Family Ochotonidae
  - *Oreolagus* nr. *O. nebrascensis* McGrew
- Family Leporidae
  - *Hypolagus?* sp.

Order Rodentia
- Suborder Sciuromorpha
  - Family Mylagaulidae
    - *Mesogaulus paniensis* (Matthew)
  - Family Sciuridae
    - *Palaeoarctomys? bryanti*, n. sp.
    - *Sciurus* sp. A
    - *Sciurus* sp. B
- Suborder Castorimorpha
  - Family Castoridae
    - *Anchitheriomys?* sp.
    - *Monosaulax*, n. sp.
- Suborder Myomorpha
  - Superfamily Geomyoidea
    - Family Eomyidae
      - *Pseudotheridomys hesperus*, n. sp.
    - Family Heteromyidae
      - *Proheteromys sulculus*, n. sp.
      - *Proheteromys* sp. cf. *P. magnus* Wood
      - *Mookomys* sp. cf. *M. formicorum* Wood
      - *Florentiamys?* sp.
  - Superfamily Dipodoidea
    - Family Zapodidae
      - *Plesiosminthus clivosus* Galbreath
      - *Plesiosminthus (Schaubeumys) galbreathi*, n. sp.

## Order INSECTIVORA

In the collections from Quarry A are numerous specimens of insectivores, unfortunately rather fragmentary. Nevertheless, this collection is quite outstanding by comparison with anything previously made known from the Miocene of North America. It is, in fact, the first collection which may be rather loosely termed an insectivore fauna, comprising, as it does, representatives of four families, seven genera, and eight to twelve species. A few over 100 specimens of limb bones, individual teeth, and jaws are listed in this report, and undoubtedly unsorted bones remain in the general collections from Quarry A. How unusual this collection is may be appreciated by reference to the published reports on North American Miocene insectivores, which, if genera and species based solely on humeri of moles are excluded, furnish records of about the same number of genera and species *in all* as from this one Colorado site. The only post-Oligocene occurrence at all comparable is the Blancan assemblage from Meade County, Kansas (HIBBARD, 1953). The naming of six new species, and the recording of four new generic records for North America also illustrates the previous paucity of insectivore material.

In the European Miocene a number of localities (e.g., La Grive-St. Alban, Viehhausen, Weisenau bei Mainz, Sansan) have produced comparably rich faunas, but the similarity to the European Miocene extends much beyond mere variety. Most of the species at Quarry A seem closely related to European species, and the entire insectivore fauna would not appear much out of place if it were recorded individually from European sediments. Thus, of the seven Quarry A genera, three seem identical with European ones *(Plesiosorex, Heterosorex, Sorex)*, and two others *(Mydecodon, Scalopoides)* may in the future be identified in Europe. Only two seem to represent lines restricted to North America *(Proscalops, Metechinus)*. Nevertheless, the fauna viewed as a unit, rather than as individual species, is a North American rather than an Old World one. Thus, (1) the only representative of the Erinaceidae is a member of the peculiar *Metechinus-Brachyerix* line which is confined to North America; (2) the Metacodontidae is at least as American as Eurasian, on present evidence, with Oligocene-early Pliocene representatives in North America; (3) *Heterosorex* is aberrant and the Heterosoricinae probably appear as early in North America *(Domnina compressa)* as in Europe; (4) *Sorex* lives today in both areas, although neither the New nor Old World fossil species seem referable to *Sorex* in a strict sense (the Quarry A *"Sorex"* species do seem generically identical with the European ones); (5) the Talpidae are characterized by the fact that they are scalopines, a characteristic New World group even if Old World representatives are known; no talpines, the characteristic Old World moles, have been recorded at Quarry A.

In part, the decided resemblance to European insectivore (and rodent) faunas is because of the facies represented. I suppose, however, that the largest single factor is the recovery method, which thus produces a record which otherwise is almost lacking. This is supported positively by even more spectacular results by washing accomplished by C. W. HIBBARD for the Plio-Pleistocene of Kansas and M. C. McKENNA for the early Eocene of Colorado. Negatively, it is supported by the fact that unlike facies are present in the several Miocene localities which show resemblances. For example, Quarry A, stream border;

La Grive-St. Alban, fissure fillings; and Viehhausen, brown coal deposits.

It has been stressed by LAVOCAT (1951, p. 34) that the European Miocene insectivore fauna is not much modified from that of the Oligocene. The Quarry A fauna also of course resembles the European Oligocene insectivore fauna. For example, *Plesiosorex* and *Heterosorex* have Oligocene representatives. There is also a decided resemblance between species of the Miocene and Oligocene of North America (as for example between *Proscalops miocaenus* and *Proscalops secundus,* and *Domnina compressa* and *Heterosorex roperi,* but the relationship seems less close than that which exists between the Oligocene and Miocene microfaunas of Europe. It is still not clear in all cases, however, what the real relationship is between certain North American and European Oligocene genera, and hence not clear as to how much of the later resemblance results from parallel descent and how much from intermigration. I assume that most of the resemblance in the Miocene results from the latter rather than the former whatever the time of migration. Hence, I do not think that genuinely separable Oligocene genera—the one American, the other European—have Miocene descendant species which I have placed here in a single genus. In any case, the range in time of several of these genera in Europe is such as to discourage very extensive use of the American insectivore fauna in geologic correlating.

## Superfamily ERINACEIOIDEA

### Family ERINACEIDAE

#### METECHINUS sp., cf. M. MARSLANDENSIS Meade, 1941

Specimen KU9988 is an isolated lower molar, either $M_1$ or more probably $M_2$, of an erinaceid. It suggests a second rather than a first molar in the backwardly slanting roots and absence of any trace of a hypoconulid. If an $M_2$, it agrees fairly well in size with that tooth in *M. marslandensis* of Nebraska (MEADE, 1941). Measurements of the ?$M_2$ (KU9988) from Quarry A are 2.5 mm. anteroposterior (ap) and 1.5 mm. transverse (tr) as compared with 2.7 mm. (ap) and 1.7 (tr), for the type specimen of *M. marslandensis.*

KU9988 also agrees in size and general shape with that of an $M_1$ of *Heterosorex roperi,* but the details of construction are all of hedgehog type. If it is an erinaceid, it is the only trace of a typical one—as in contrast to the metacodonts—in the Quarry A collection. In confirmation of its erinaceid position is the fact that the root area has the ridges and depressions characteristic of typical hedgehogs, and lacking or only incipiently developed in other insectivores from Quarry A.[4] There is no reason to suppose that KU9988 is a deciduous tooth.

The reference of a tooth fragment to *Brachyerix* by GALBREATH (1953, p. 92) is probably in error. The fragment cannot be identified with certainty as that of an insectivore.

## Superfamily SORICOIDEA

### ?Family METACODONTIDAE

BUTLER (1948, p. 491) has proposed the family Metacodontidae for the genera *Metacodon, Plesiosorex,* and *Meterix.* He thinks (oral communication) that the group is soricoid rather than erinaceid. Specimens from Quarry A provide a record of the presence of the hitherto Old-World genus *Plesiosorex,* and add certain anatomical features to our knowledge of this genus which lends support to BUTLER's thesis that *Plesiosorex* is soricoid rather than erinaceid in affinities. Two species are probably present. The smaller, rare and fragmentary, is not named specifically at present.

#### PLESIOSOREX COLORADENSIS Wilson, n.sp.

Figures 9-13

*Holotype.* Incomplete left lower jaw with $P_4$-$M_1$ and alveoli for the other teeth, No. 9989 Univ. Kansas Mus. Nat. Hist. Also almost surely part of the same individual, a right lower jaw with $I_2$ and $P_4$.

*Referred specimens.* Cranial fragment bearing right $P^4$-$M^1$ and left $P^3$-$P^4$, KU9990; and individual teeth as follows, KU9991 $P^3$; KU9992-KU9993 $P^4$; KU9994 $M^1$; KU9995 $M^2$; KU9996 $P_3$?; KU9997 $P_4$; KU9998-KU9999 $M_1$; and KU10001-KU10004 $M_2$; KU10005 ?$DP^3$.

*Geological age and locality.* Silty sands in the Pawnee Creek Formation that are regarded as the equivalent of the Marsland of Nebraska. Martin Canyon local fauna, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Specific diagnosis.* A species of *Plesiosorex* with complete dentition, $P_3$ with two roots, $M_1$ lacking external cingulum (or only a faint trace of one), and with the posterior of two mental foramina beneath the anterior root of $M_1$.

*Description.* The dentition of *Plesiosorex* has been described adequately by VIRET (1940, 1946) and by SEEMAN (1938), and need not be dealt with here except briefly as it relates to P. *coloradensis.* The dental formula is complete; the present specimens merely confirm

[4] In respect to the alveolar grooving of hedgehogs, the presence of it may not be definitive. Bony excrescences, which seem quite the same to me as those of the hedgehogs, are present in some individuals of *Sorex grivensis.*

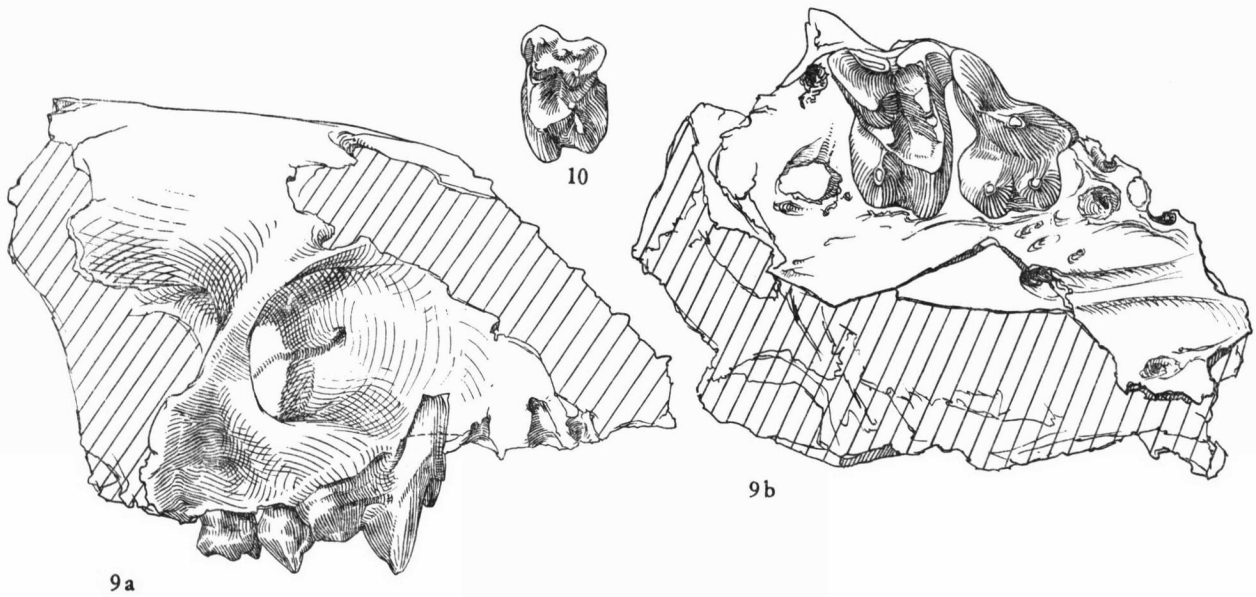
VIRET's (1946) statement in this. If KU9996 is a $P_3$ to be assigned to *P. coloradensis,* then $P_3$ bears two roots although apparently these occupied a common socket in the jaw. The socket in KU9989 suggests rather vaguely actually that something other than a single root was present. $M_1$ of *P. coloradensis* differs from that in described specimens of *Plesiosorex* in lacking an external cingulum except for a minute cusplike structure at the base of the paraconid. $M_1$ has a mesostylid cuspule that may also be seen in $M_1$ of *P. soricinoides* (St. Andre, Mar. 228), and *P. styriacus* (THENIUS, fig. 5, 1949). In $M_2$ the external cingulum is somewhat variable but is more strongly developed than in $M_1$, and perhaps ranges from weaker than in European species of *Plesiosorex* to essentially comparable in this regard. A small, but quite definite, hypoconulid is present in $M_1$ and $M_2$ of unworn teeth. Its presence could not be observed in a tooth much worn.

$P^3$ has a strong paracone cusp, a relatively small protocone directly internal to it, a minute parastyle, and a fairly prominent metastyle (much lower than the paracone). A prominent internal ledge slopes backward and downward from the protocone. KU10005 is evidently a posterior upper deciduous premolar of a large insectivore, probably $Dp^3$ of *P. coloradensis.* It differs from $P^4$ principally in the much less developed lingual part. Protocone and hypocone are present, but rudimentary. (ap diameter: KU10005: 3.2+; tr diameter: 2.5.)

$P^4$ is a much larger tooth than $P^3$ but the basic structure is the same. The parastyle is small. The paracone is a high prominent cusp. The metastyle in $P^4$, however, is a much stronger blade than in $P^3$, being in fact of more mass than the paracone, but not rising nearly so high. The protocone is a distinct cusp slightly more anterior to the paracone than is the case in $P^3$. The ledge posterior to the protocone is expanded, and bears a hypocone cusp essentially comparable in size to the protocone.

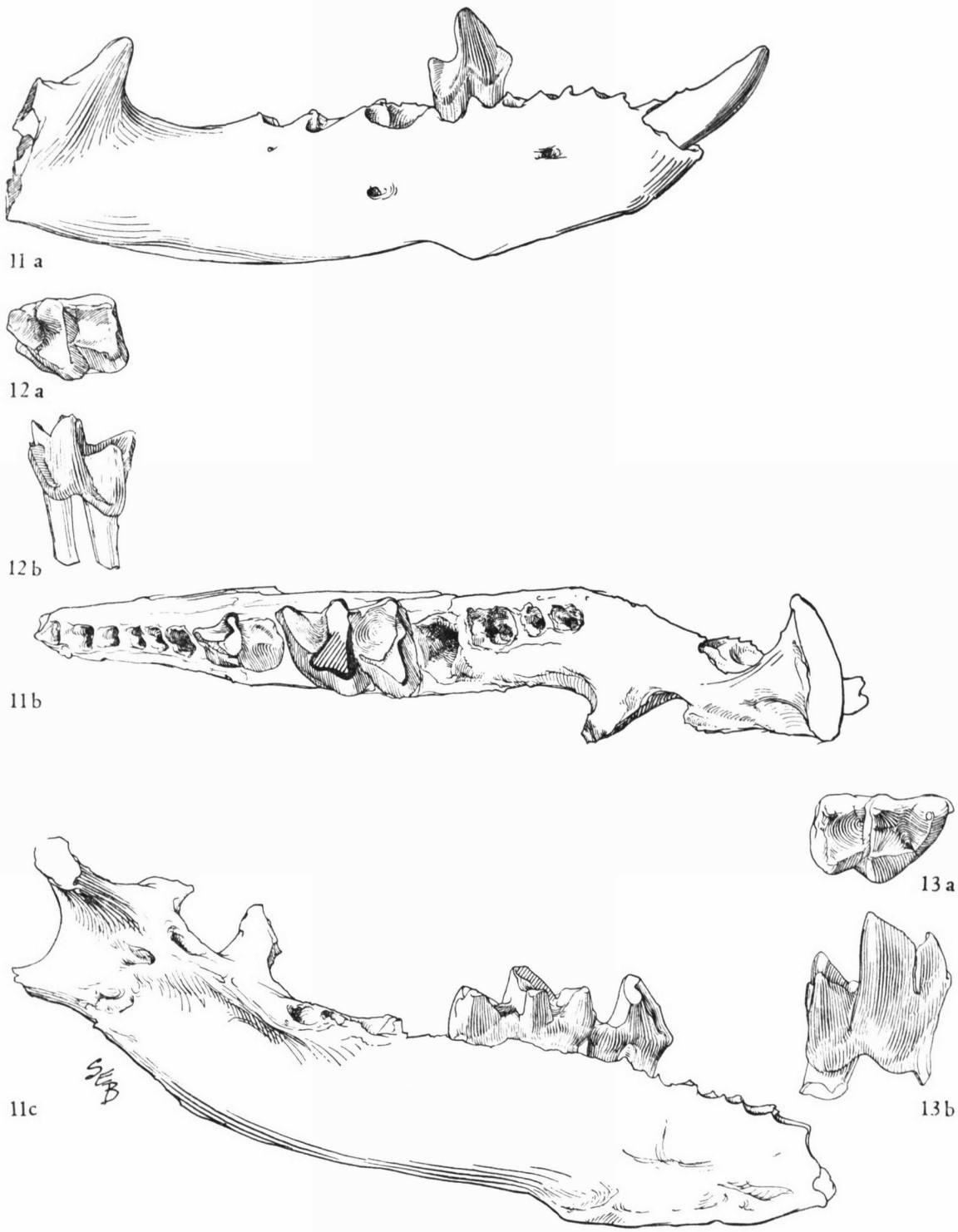
$M^1$ is extended transversely as it is in all molars of *Plesiosorex.* The principal external cusps (paracone and metacone) are set in from the labial margin, and the external shelf resulting from this position bears prominent parastyle, mesostyle, and metastyle structures. Both conules are present, but the metaconule is perhaps the more persistent with wear. The hypocone is a large cusp equalling the protocone in size.

$M^2$ differs from $M^1$ chiefly in smaller size, and the relatively smaller size of the hypocone. In the single specimen available, the mesostyle consists of two cusps.




FIGURES 9, 10. *Plesiosorex coloradensis,* all ×6.————9a, Lateral view of skull fragment KU9990; 9b, occlusal view of same.————10, Occlusal view of left $M^2$, KU9995.

In none of the molars, either upper or lower, is there more than faint traces of the ridges characteristically developed on the median sides of the roots in typical erinaceids. Consequently, the alveoli for the molars lack any trace of grooves (BUTLER, 1948, p. 492). $P^4$ has three roots: one for the paracone, one for the metastyle, and one underneath the protocone-hypocone. $M^1$ also has two external roots, and a single internal one, but this latter is deeply grooved on its internal surface. The same root structure is present in $M^2$ as in $M^1$.




FIGURES 11-13. *Plesiosorex coloradensis,* all ×6.————11, Type specimen, KU9989; 11a, lateral view of right ramus; 11b, occlusal view of left ramus; 11c, medial view of left ramus.————12a, Occlusal view of left $M_2$, KU10002; 12b, lateral view of same.————13a, Occlusal view of right $M_1$, KU9998; 13b, lateral view of same.

The lower jaw presents only one point of difference from previously described specimens of *Plesiosorex*. The posterior of the two mental foramina is under the anterior root of $M_1$ rather than the anterior root of $P_4$ as is the case in Oligocene and Aquitanian species. [In St. G. 840 Chavroches the posterior foramen is under the extreme posterior part of $P_4$.] This feature is, however, duplicated in the late Vindobonian and Sarmatian species, *Plesiosorex styriacus*. [*Plesiosorex germanicus* is a synonym of *P. styriacus* according to THENIUS (1949, p. 685).] Figures and descriptions of specimens of *P. styriacus* do not depict or mention an anterior foramen, but the posterior one is placed as in the New-World species (SEEMANN, 1938; THENIUS, 1949).

The skull of *Plesiosorex* has not been previously described, and KU9990 is hence of great interest because a small part of the skull is preserved.

Dorsally only the interorbital area is preserved. This suffices to show that there is little interorbital constriction, that a low sagittal crest is present, and finally that there may have been supraorbital ridges. If the ridges are present, they are rather far forward, the divergence from the sagittal line not taking place much back of a point opposite the anterior border of the orbital fossae.

The side of the skull in the region of the zygomatic root of the maxillary is also preserved. The molars relative to the position of the anterior edge of the orbit, and the root of the zygomatic arch are relatively far forward in comparison to the position of the molars in the Erinaceidae generally. Some genera, nevertheless, such as *Echinosorex* and *Padogymnura* have essentially comparable conditions (BUTLER, 1948). What is really noteworthy about this part of the skull is the extremely large infraorbital canal. Enlargement of the canal has reduced the facial part of the maxillary between the anterior opening of the canal and the orbit to a narrow bar of bone situated opposite the posterior border of $M^1$. The skull is deeply excavated at the entrance to the canal. These features are unlike those in typical erinaceids, and are much more nearly like those of various primitive (zalambdodont) insectivores and of shrews. The snout was presumably sensitive and highly flexible. Seemingly also because of the enlargement of the infraorbital canal, the lacrimal foramen is dorsal in position and lies anterior to the orbit and somewhat anterior to the entrance of the infraorbital canal. The maxillary root of the zygoma is opposite the anterior part of $M^2$. As preserved, although not peglike, there is no real evidence that the zygoma continued posteriorly as a complete arch, but it presumably did so.

*Comparative Measurements of* Plesiosorex coloradensis, *in Millimeters*

| | *P. coloradensis* | *P. "germanicus"* | *P. cfr. soricinoides* | *P. soricinoides* | *Meterix latidens* |
|---|---|---|---|---|---|
| $P^3$, ap | 2.2?-2.4 | ..... | ..... | ..... | ..... |
| tr | 2.0 | ..... | ..... | ..... | ..... |
| $P^4$, ap | 3.1-3.5 | ..... | ..... | ..... | ..... |
| tr | 4.2-4.6 | ..... | ..... | ..... | ..... |
| $M^1$, ap | 3.3-3.4 | 3.0 | ..... | ..... | 2.7 |
| tr | 5.0 | 5.1 | ..... | ..... | 4.0 |
| $M^2$, ap | 2.3 | ..... | ..... | ..... | ..... |
| tr | 3.6 | ..... | ..... | ..... | ..... |
| $I_2$, ap | 1.5 | 2.1 | ..... | 1.3 | ..... |
| tr | 1.0 | 1.2 | ..... | ..... | ..... |
| $P_3$, ap | 1.8 | ..... | ..... | 1.3 | ..... |
| tr | 1.2 | ..... | ..... | 1.1 | ..... |
| $P_4$, ap | 2.3-2.5 | 2.7 | 2.3 | 1.7 | 1.8 |
| tr | 1.3-1.6— | ..... | 1.34 | 1.3 | ..... |
| $M_1$, ap | 3.9-4.0 | 3.8-4.8 | 3.3 | 2.5 | ..... |
| tr | 2.5-2.6 | 2.3-2.4 | 2.3 | 1.9 | ..... |
| $M_2$, ap | 2.7-3.1 | ..... | ..... | ..... | 3.0 |
| tr | 2.2-2.5 | ..... | ..... | ..... | 2.4 |
| Depth of jaw beneath $M_1$ | 4.4 | ..... | ..... | ..... | 4.5 |
| Length of jaw, post. edge of condyle to ant. edge of alveolus for $I_2$ | 22.0 | ..... | ..... | ..... | ..... |
| Alveolar length, $I_3$-$P_4$ | 6.8 | 6.7-6.8 | 7.6 | 10.0 | 5.7 |
| Alveolar length, $M_1$-$M_3$ | 8.5 | 8.0-9.5 | 7.0 | 7.8 | 9.0 |

As represented in KU9990, the palate is moderately concave between the premolars, and has a median ridge in this area. A pair of large foramina are present opposite the anterior edge of $P^4$. If these are anterior palatine foramina they are exceptionally far forward. The lateral margins of the palate are pitted after the manner of those of certain shrews (for example, *Crocidura*).

*Affinities.* I think it is clear that the Colorado species is to be assigned to the *Plesiosorex-Meterix* group. Not a single character is seen that is not found also in one or another of the previously described species. Of the two genera, *Plesiosorex* and *Meterix* (HALL, 1929), *P. coloradensis* is structurally closer to the former, but it could well be ancestral to *Meterix*. So far as the scant material of *Meterix* permits comparison, the new species differs from it only in characters which can readily be regarded as more primitive. Thus, *Meterix* in comparison with *P. coloradensis* shows the following features: (1) a dental formula of $\frac{2.1.3.3}{}$ rather than $\frac{3.1.4.3}{}$; (2) judging from published figures, that the dental foramen and overlying ridge of *Plesiosorex* is intermediate between those of *Meterix* and *Erinaceus;* (3) a comparable size, but *P. coloradensis* somewhat smaller (5-10 percent in length of tooth-row); (4) single-rooted, rather than double-rooted $P_3$; and (5) the reduction in dentition, length of $I_3$-$P_m$ seems to be shorter relative to the length of the molars (ratio of 0.80 in *P. coloradensis* and 0.56 in *Meterix*).

There is, I think, more difference between *Meterix latidens* and *P. coloradensis* than between the latter and the type species of *Plesiosorex, P. soricinoides.* Consequently, I assign *coloradensis* to the European genus.

*Plesiosorex soricinoides* (VIRET, 1940, 1946) is of Oligocene (Stampian) age. I judge it to be more primitive (or less specialized) than *P. coloradensis* in its relatively more developed premolar region. The ratio of $I_3$-Pm/$I_3$-$M_3$ length is 0.56 in contrast to 0.44 in *coloradensis.* On the other hand, $P_3$ is single-rooted in *P. soricinoides* and double-rooted in *P. coloradensis.* Both $P_3$ and $P_4$ in *P. soricinoides* are relatively broader; broadness may be a less specialized feature of *P. soricinoides* since the known post-Stampian species have thinner, more delicate $P_3$-$P_4$. An additional feature which may reflect geologic age is the position of the posterior mental foramen. In *P. styriacus* ("Sarmation"), *P. coloradensis,* and *Meterix* (early Pliocene), the foramen is under the anterior part of $M_1$, but in the Stampian and Aquitanian species usually is under the corresponding part of $P_4$. If length of $M_1$ can be taken as a guide to size, the New-World species is considerably larger, but the tooth-bearing part of the lower jaw may be slightly shorter. *P. soricinoides* has a distinctly greater development of the external cingulum of $M_1$.

*P. cfr. soricinoides* from Chavroches (Aquitanian) has a double-rooted $P_3$ like that of the New-World genus, and the resemblance otherwise is close, except that in *P. cfr. soricinoides*: (1) the posterior mental foramen is under the extreme posterior part of $P_4$ rather than under $M_1$; (2) the external cingulum of $M_1$ is better developed; and (3) the Pm region is less reduced, being intermediate in this respect between *P. soricinoides* and *coloradensis.*

I suppose that the Marslandian species is more advanced (if only slightly) than the Aquitanian one.

*Plesiosorex styriacus* from Viehhausen bei Regensberg and the Styrian brown coals (late Vindobonian and Sarmation) is the youngest European representative of the genus. It differs from *P. coloradensis* in: (1) presence of strong external cingulum on $M_1$; (2) slightly more robust hypocone on $M^2$, but, paradoxically with less of an indentation of the posterior margin; (3) possibly a relatively more robust $I_2$. The single $I_2$ known of *P. coloradensis* is smaller than is indicated by SEEMANN for *P. styriacus.* Measurements of other teeth are variable enough to include those of *P. coloradensis*; and (4) possibly three rather than four premolars. SEEMANN (1938, p. 32) thought that four premolars were present, $P_3$ being single-rooted. VIRET (1940) concluded that the alveoli regarded by her as for $P_2$ and $P_3$ were actually for a single double-rooted tooth. Examination of the available illustrations suggest that VIRET is correct. THENIUS (1949, p. 689) has also thought this to be the case. If so, there is one less premolar in the Vindobonian and Sarmatian species. STROMER (in SCHREUDER, 1940, p. 327) concluded that *"P. germanica"* "had then so great an affinity with *Meterix latidens* HALL (1929) from the Pliocene of Nebraska [*sic*], that it had to be named *Meterix germanica* SEEMANN".

*P. styriacus* closely resembles *P. coloradensis* in size and in position of the posterior mental foramen. There is some suggestion in points (3) and (4) of the above that *P. styriacus* is more progressive. This would be in harmony with the general thesis that the Quarry A mammals are of Burdigalian or early Vindobonian age. It is also possible that *Plesiosorex* is not a suitable species for use in close correlation.

An American species equivalent in age to *P. coloradensis* is *Metechinus marslandensis* described by MEADE from the Marsland of Nebraska. The type and only known specimen is a jaw fragment bearing $M_1$-$M_2$. This fragment does not seem to pertain to the genus *Plesiosorex.* In any case the Nebraska and Colorado specimens are specifically separable on the basis of such characters as the presence of an external cingulum on $M_1$ of *M. marslandensis,* the greater reduction of $M_2$ in respect to $M_1$, and some other features.

*Plesiosorex* is known from the Oligocene of Europe (there is a tentative record also in Asia, LAVOCAT, 1951, p. 18): its type species is of course from this series (Chauffours, France).

It may be suggested then that sometime in early Miocene time a stock migrated into North America to

give rise to *P. coloradensis* and through it to *Meterix latidens*. Essentially this view has in fact been proposed earlier by VIRET (1940, p. 40), but he thought the migration occurred just preceding the Pontian. Is there possibly reason to believe that this view is not correct? *Metacodon* of the North American Oligocene has been suggested (BUTLER, 1948) as a relative of *Plesiosorex*. Could *Metacodon* rather than European species of *Plesiosorex* be the ancestor of *P. coloradensis*? The genus *Metacodon* has been made well known by the work of PATTERSON & MCGREW (1937). It is clearly distinct from *Plesiosorex* although a number of its characters are simply primitive, for example: the lack of specialization of $I_2$, the smaller hypocones of the molars, and the double-rooted premolars. But there are some features that can not be so interpreted, and these prevent consideration of *Metacodon* as ancestral to the American species. $P_2$ is distinctly larger than $P_3$, and in the upper molars protoconules are absent, and metaconules absent or very small, in this regard resembling *Saturnalia* STEHLIN.

### Affinities of *Plesiosorex* and Metacodontidae

*Metacodon* was assigned originally by its author, CLARK (1937, p. 310), to the Leptictidae. Later, PATTERSON & MCGREW transferred the genus to the Erinaceidae. *Plesiosorex* and *Meterix* have been regarded as members of the Erinaceidae by most authors. BUTLER (1948, p. 491), however, has called attention to a number of characters, in these genera, which are unlike those of typical hedgehogs. He felt that the evidence for assignment of these genera to any existing family was so poor that he was justified in erecting a new family Metacodontidae. Subsequently both GALBREATH (1953, p. 43) and SIMPSON (1951, p. 16) have objected to this procedure. The matter may be reconsidered in the light of the additional materials, particularly the skull fragment, now available.

There are a number of similarities which seem to relate *Metacodon, Plesiosorex,* and *Meterix* to one another, and the known differences are no greater than among genera of undoubted hedgehogs. Thus, the argument can reasonably be based on *Plesiosorex,* although it must be held in mind that *Metacodon* is the type genus. [SIMPSON (1951, p. 16) fails to see any particular resemblance between *Metacodon* and *Plesiosorex.*]

*Plesiosorex* shows the following characters which are either unknown in any certainly erinaceid genus, or are atypical of the Erinaceidae: (1) infraorbital canal greatly enlarged; (2) paracone and metacone of upper molars internal in position, and consequently a broad external shelf is present which has well-developed styles, these teeth being extended transversely; (3) lacrimal foramen of pronounced dorsal and anterior position lying outside the orbit proper and in advance of entrance to infraorbital canal; (4) condyle of low position and coronoid process with the anterior edge rising sharply vertically; (5) lack of grooving in the alveoli of molars; and (6) temporal musclature of anterior origin (anterior position of supraorbital ridges and termination of sagittal crest).

These features, in varying degree, can be found in the soricoid insectivores (BUTLER, p. 474, 1956). Most of them are found also in certain primitive (zalambdodont) insectivores, but the "Metacodontidae" obviously do not belong in that group. They just as obviously are not shrews, and although *Plesiosorex* has at times been regarded as a mole, the molar paracone and metacone have not assumed a chevron shape.

Additional features possessed by *P. coloradensis* (possibly not altogether constant in the "family") that are nonerinaceoid and usually soricoid may be listed: (1) anterior position of upper molar dentition; (2) posterior position of posterior mental foramen; (3) large anterior palatine foramina far forward (opposite anterior half of $P^4$); (4) absence of an anterior cingulum (except for vestige) in $M_1$, as in *Talpa*; (5) pitting and wrinkling of the bone of palate, as in *Crocidura*; and (6) possibly the zygomatic arch is incomplete. Additionally it may be noted that the presence of two mental foramina is not common in the hedgehogs and that *Plesiosorex* differs from members of the Echinosoricinae with which group it shares some characters in lacking divided inner roots on the upper molars.

In *Plesiosorex* $I_2$ is enlarged; the series $I_3$-$P_3$ slants forward and becomes imbricating at its anterior end. VIRET (1946, p. 315) has compared the anterior teeth in *Plesiosorex* to those of shrews. It seems to me that the entire anterior tooth-series suggests more a beginning of a soricid arrangement than of an erinaceoid.

*Saturninia* STEHLIN (1940) of the latest Eocene (upper Ludian) was described by its author as a shrew, and this assignment was maintained by SIMPSON (1945). STEHLIN (p. 306) recognized that his genus, although showing intermediate features between *Sorex* and generalized insectivores, was not directly ancestral to living shrews; among other pertinent objections to its being directly ancestral was its too-late geological age. As a matter of fact, *Saturninia* can hardly be referred to the Soricidae in a strict sense for the paracone and metacone do not form the W-shaped ectoloph characteristic of the group. In fact, greater resemblance is shown to the metacodontids than to the soricids (a conclusion reached independently by PATTERSON), although *Saturninia* probably is not to be considered among the possible ancestors of *Plesiosorex*. *Saturninia* has some features (for example, weak conules and possibly structure of hypocone) that are closer to those of the Soricidae than to those of *Plesiosorex*.

*Saturninia* agrees with *Plesiosorex* in the following

important characters: (1) structure of $P^4$, except that it is distinctly more primitive in the higher, almost styliform, paracone; and (2) upper molars with noncrescentic outer cusps which, however, tend to be set in from the external edge of the teeth. There is also a general agreement in tooth pattern, which may only indicate relatively primitive structures in both. More pertinent, perhaps, are the apparent differences of which the following seem to be the most important: (1) the much less well-defined conules of *Saturninia*; and (2) more or less molariform $P_4$ in *Saturninia,* and hence more leptictidlike structure of this tooth. Nevertheless, *Saturninia* shows some variation, and the $P_4$ of *Plesiosorex* possibly is a modification from *Saturninia.* In any case, whatever the taxonomic value of the resemblances and differences in *Saturninia* and *Plesiosorex,* both genera exhibit some soricoid features but without either of them possessing certain critical features that would permit outright assignment to the Soricidae (or to the Talpidae).

Dr. BUTLER (oral communication) has suggested that *Nesophontes* (ANTHONY, 1916) should be studied as a possible ally of *Plesiosorex. Nesophontes* recently has been studied in detail and compared with *Solenodon* by MCDOWELL (1958) who concludes that *Nesophontes* and *Solenodon* are closely related, and are soricoids. SABAN (1954) and BUTLER (1956) have united the superfamilies Tenrecoidea, Soricoidea, and Chrysochloroidea as a separate suborder of insectivores, the Soricomorpha. MCDOWELL supports this arrangement except for regarding the Chrysochloridae as assignable to the Tenrecoidea.

*Plesiosorex* resembles *Nesophontes* and *Solenodon* in some features, but differs sharply in others. For example, *Plesiosorex* is more primitive than *Nesophontes* in lacking a V-shape to the metacone of the upper molars, and in possessing a simple condyle in the lower jaw: the former genus is more advanced in having large hypocones in the upper molars and a more complex $P^4$. *Plesiosorex* can have no direct phylogenetic relationships with either *Nesophontes* or *Solenodon.*

Many of the characteristics of the Soricomorpha are found in *Plesiosorex,* and there is much to be said for BUTLER's view (oral communication, 1956) that (1) the metacodontids are not hedgehogs, and (2) that they may be related to the soricoids. The metacodontids may be placed provisionally in the group Soricomorpha as one of the families of Soricoidea, although a notably primitive one.

#### PLESIOSOREX? sp. (small form)

Two isolated second lower molars, KU10006 and KU10007, closely resemble *P. coloradensis* except in size. Wear on the crowns prevent detailed comparisons with those of *P. coloradensis,* and in any case it would be inadvisable to name such fragmentary specimens. In size, these teeth agree with those of *Heterosorex roperi,* but have more inflated crowns, and less developed external cingula. Measurements (in mm.) are: anteroposterior diameter, 2.0, 2.1; transverse diameter, 1.6, 1.7.

### Family SORICIDAE

The shrews from Quarry A fall into two well-marked divisions; *Heterosorex* representing one, and *Sorex* the other division. VIRET & ZAPFE (1951) have made *Heterosorex* the type of a distinct subfamily Heterosoricinae, and I have followed them in this, although I am not certain that so doing is making an excessive separation, if the remaining shrews are grouped together in the Soricinae (as seemingly advocated by VIRET & ZAPFE).

### Subfamily HETEROSORICINAE

This rather rare group of shrews in Europe is represented here by the commonest species of insectivore *(Heterosorex roperi)* in Quarry A. The American species may have descended from an early Oligocene species of *Domnina* through *D. compressa* but more complete material of *Domnina* is needed to establish this as more than a probabilty. In any case, *Heterosorex* itself represents a strongly aberrant line. Two species seemingly are present at Quarry A, a common large one, and a much rarer, smaller one (not formally named) that may have certain distinctive structural features in addition to size.

#### HETEROSOREX ROPERI Wilson, n.sp.

Figures 14-22

This species is named in honor of Mr. Albert B. Roper of West Plains, Colorado.

*Holotype.* No. 10008 Univ. Kansas Mus. Nat. Hist., left lower jaw with $M_1$-$M_3$, but lacking the symphyseal part. An incisor, now broken out of the jaw is provisionally associated with the specimen.

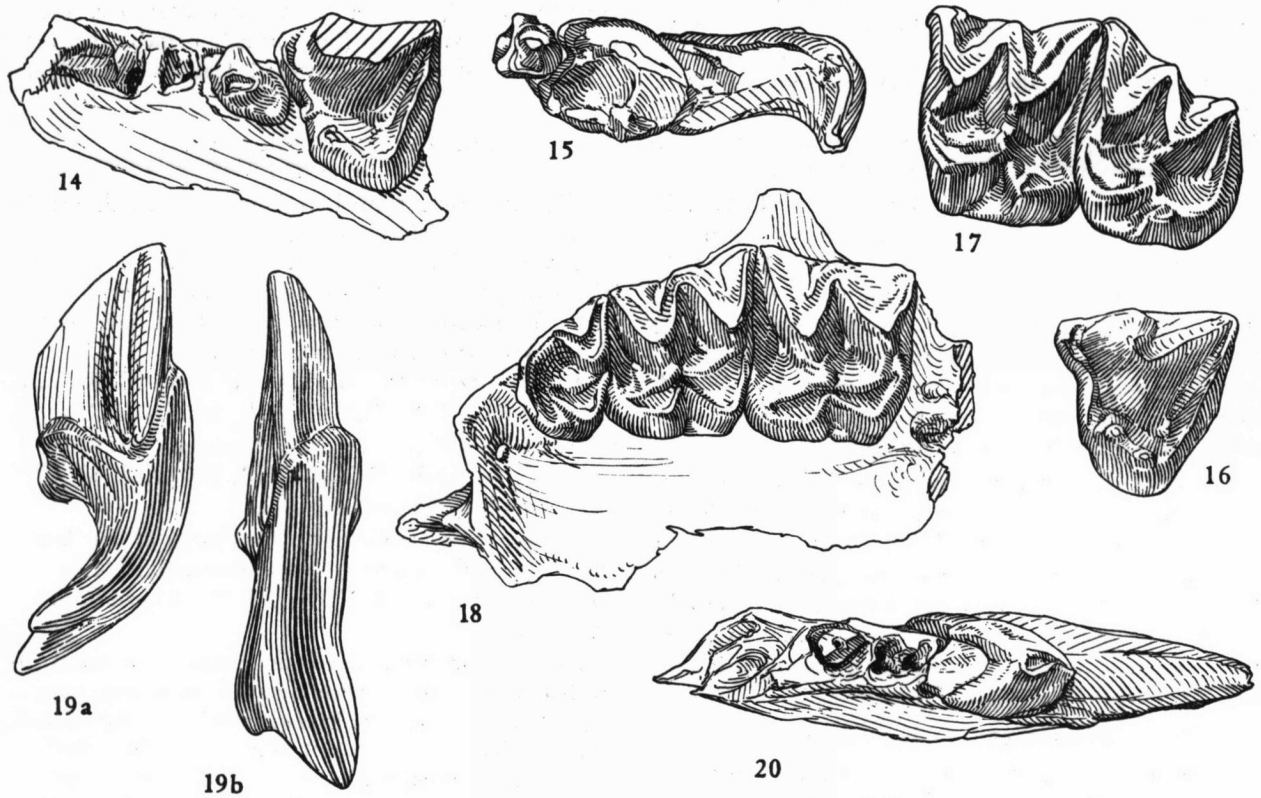
*Referred specimens.* KU9281, KU10009-KU10012, $\underline{I}$; KU10013-KU10014, KU10019, $P^4$; KU9280, KU10015, KU10016-KU10018, upper jaw fragments; KU10020, $\underline{I}$; KU10021, $M_1$; KU10022-KU10024, $M_2$; KU9282, KU10025-KU10033, lower jaws.

*Geological age and locality.* Silty sands of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼, sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Specific characters.* Size as in *Heterosorex sansaniensis,* but larger than *H. neumayrianus.* Transverse process of palate better developed laterad than in *H. sansaniensis.* Upper molars ($M^1$ and $M^2$) slightly broader relatively than in *H. sansaniensis* with protocone and hypocone more cuspidate. Anterior border of ascending ramus of lower jaw possibly more nearly vertical than in *H. sansaniensis.* Lower canine and two or three premolars, possibly as in *H. neumayrianus* and possibly with one additional tooth as compared with *sansaniensis.*

*Description.* The skull is practically unknown in the new species. What is preserved shows that *H. roperi* probably agrees with the type of the genus, *Heterosorex sansaniensis,* in possessing a complete zygomatic arch. The anterior part of the arch preserved in our specimens is a well-developed spine—much more of a one than in existing soricids. The palate is partly preserved and has a well developed, transverse crest terminating it posteriorly. This crest is better developed than in *H. sansaniensis,* if it is not subject to individual variation. The teeth show no evidence of pigment that is convincing. *Domnina* has heavily pigmented teeth, and GAILLARD (1915) and ZAPFE (1951) reported the presence of pigment in *Heterosorex sansaniensis.* I suspect that the Colorado species was pigmented, for its relation to them, and particularly to *H. sansaniensis,* is clear. The dental formula of *H. roperi,* although somewhat uncertain, may be written tentatively as $\frac{3.0.3.3}{1.0.4.3}$, or $\frac{2.1.3.3}{1.1.3.3}$. For purposes of description, I assume the latter to be true.

$I^2$ resembles that of *H. sansaniensis* in bifid structure. Serving functionally to take the place of the weak basal cuspule of $I^2$ is the large (relative to $\underline{C}$) $I^3$. So far as comparisons can be made, this tooth is exactly like that of *Heterosorex* of the Sansan unless the external cingulum in the Colorado species is better developed. $I^3$ and the one following have been described by GALBREATH (1953, p. 92) under the name "Soricid, ?n. gen. and sp.," and the description need not be repeated here except to emphasize the smallness of $\underline{C}$ relative to $I^3$. In the Oligocene *Domnina,* which has many points of resemblance to *Heterosorex,* $I^3$ and $\underline{C}$ are not obviously (from their alveoli) different in size. $P^2$ is essentially comparable in size and shape to $\underline{C}$. $P^3$ has not been previously described in the genus *Heterosorex.* This tooth in *H. roperi* is nearly comparable in area to $\underline{C}$, but is rather narrowly oval in outline. It has a principal cusp anteroexternally, and a rather considerable heel area. The long axis of the tooth is somewhat obliquely placed, and measurements made along or at right angles to the tooth-row are perhaps misleading. Judging from the alveoli of $I^3$-$P^2$ of *H. sansaniensis,* the type species had comparable-sized teeth.




FIGURES 14-20. *Heterosorex roperi,* all ×11.————14, Occlusal view of left $P^3$-$P^4$, KU10015.————15, Occlusal view of right $I^2$-$\underline{C}$, KU9280.————16, Occlusal view of left $P^4$, KU100019.————17, Occlusal view of left $M^1$-$M^2$, KU10018.————18, Occlusal view of right $M^1$-$M^3$, KU10016.————19, Right $I^2$, KU10010; 19a, external view; 19b, anterior view.————20, Occlusal view of left $\underline{I}$-$\underline{C}$, KU10029.

$P^4$ has not been described except in the broadest terms. There does not seem to be much if any difference in the structure of $P^4$ in *H. roperi* and *H. sansaniensis*. The principal cusp is the paracone (parametacone) flanked by a well-developed metastyle. A minute parastyle is present. A heavy ridge encircles all but the external border of the tooth, and a small protocone and a very indistinct hypocone are eminences on this ridge.

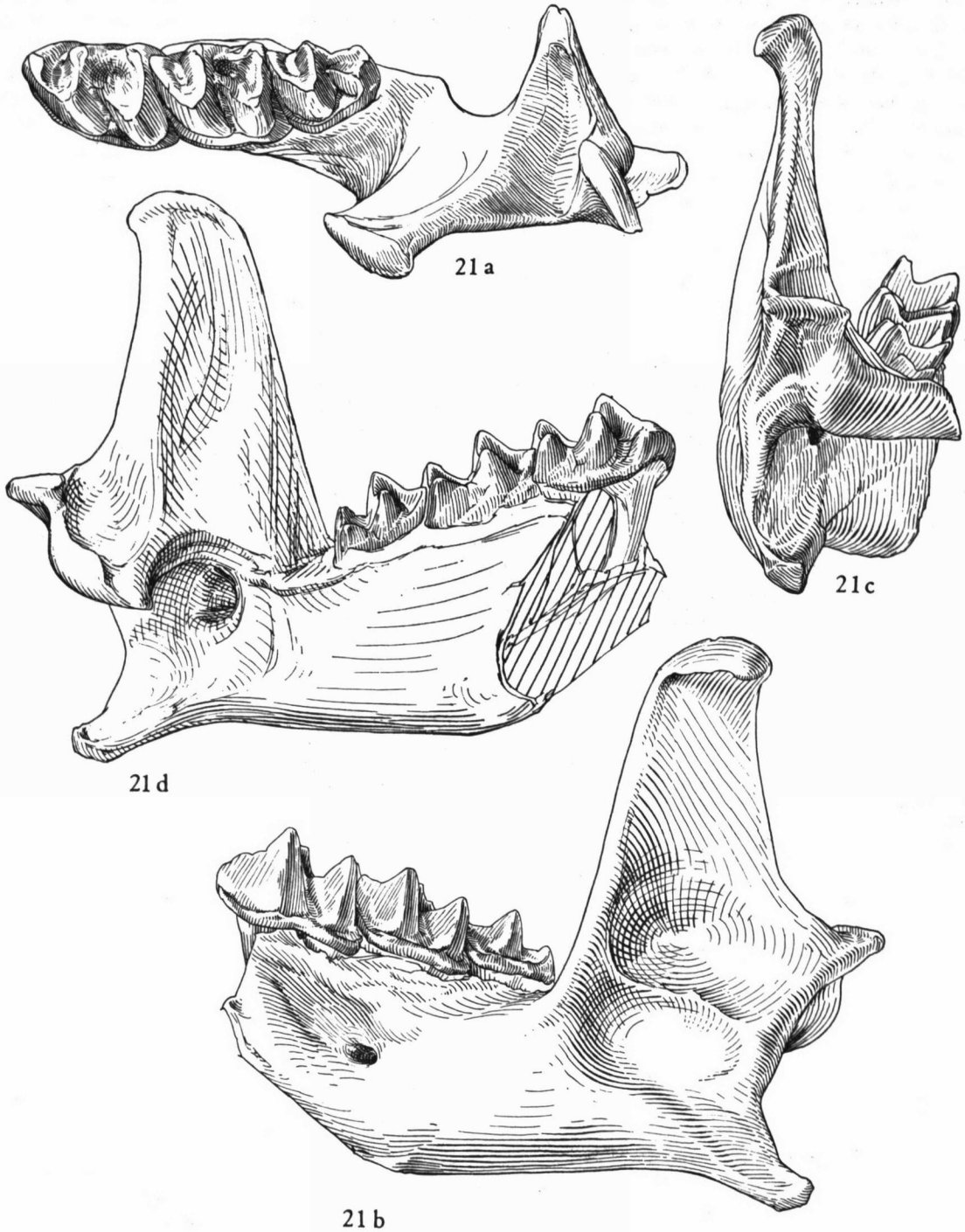



FIGURE 21. *Heterosorex roperi*, all ×10. Type specimen, left ramus with $M_1$-$M_3$, KU10008; 21a, occlusal view; 21b, lateral view; 21c, posterior view; 21d, medial view.

Wear would easily obscure the presence of the hypocone (it might be absent as an expression of individual variation), and with more wear the protocone would hardly be identifiable. Insofar as it is preserved, the $P^4$ of *Domnina* is similar.

As in *Domnina,* the molars of *Heterosorex roperi* have a striking resemblance to those of the Recent *Blarina.* Also as in the former, the only observable difference in the structure of $M^1$ and $M^2$ lies in the extension externally of the posterior cingulum—in *Domnina* to a point "immediately posterior to the metastyle" (PATTERSON & MCGREW, 1934, p. 249), and essentially to the same place in *Heterosorex.* $M^1$ and $M^2$ seemingly differ from those of *H. sansaniensis* in their slightly greater breadth, and more importantly in being more cuspidate. $M^1$ from the Sansan has a slightly divided mesostyle lacking in the Quarry A species. $M^3$ seems quite the same as that in *H. sansaniensis* as far as it is possible to compare the two.

The lower jaw of *Heterosorex roperi* is characterized by several features more or less diagnostic of the genus: (1) the position of the mental foramen under the anterior root of $M_2$, and at the posterior end of a considerable depression in the side of the jaw; (2) the large incisor the root of which extends back to a point beneath $M_2$, (3) the high coronoid process having a deep masseteric fossa, but lacking an intertemporal (posterointernal ramal) fossa on the inside of the jaw; and (4) the general stoutness of the jaw. In this connection, *H. roperi* shows one feature figured by ZAPFE (1951, p. 463, fig. 4), which has not been mentioned by previous authors even when they commented on the presence of a considerable masseteric depression—the division of the masseteric depression into superior and inferior parts by a ridge of bone crossing the fossa at a level about two-thirds of the way down from the superior border. The upper of the two parts is distinctly the deeper. The anterior edge of the coronoid process is nearly perpendicular to the horizontal ramus. The corresponding part in *H. sansaniensis* slopes backward slightly. The posterior edge of the coronoid slopes forward in *sansaniensis* to a greater degree. In L. Gr. 209 (Basel collections) this results in a less robust process. However, in Ss 603 (Basel collections) the coronoid process is nearly if not quite identical to *H. roperi.* The condyle of the type of *H. delphinensis* has suffered considerable damage, but appears weaker. The condylar articulations, although not much separated, are clearly double, thus agreeing with the complex glenoid fossa of the skull of *H. sansaniensis* redescribed and refigured by VIRET & ZAPFE (1951, fig. 11, p. 423-424). These articulations are slightly advanced over those of *Sorex vireti* in degree of separation, which is perhaps not expected in view of the supposed complete zygomatic arch of *Heterosorex.*

The enlarged incisor tusk appears to be much the same in *H. roperi* as in the European species. Perhaps the dorsal crenulations are more subdued (the type of *delphinensis* has these well displayed).

One of my specimens, KU10029, has the $\overline{C}$ preserved, the first time this tooth has been recovered in *Hetero-*

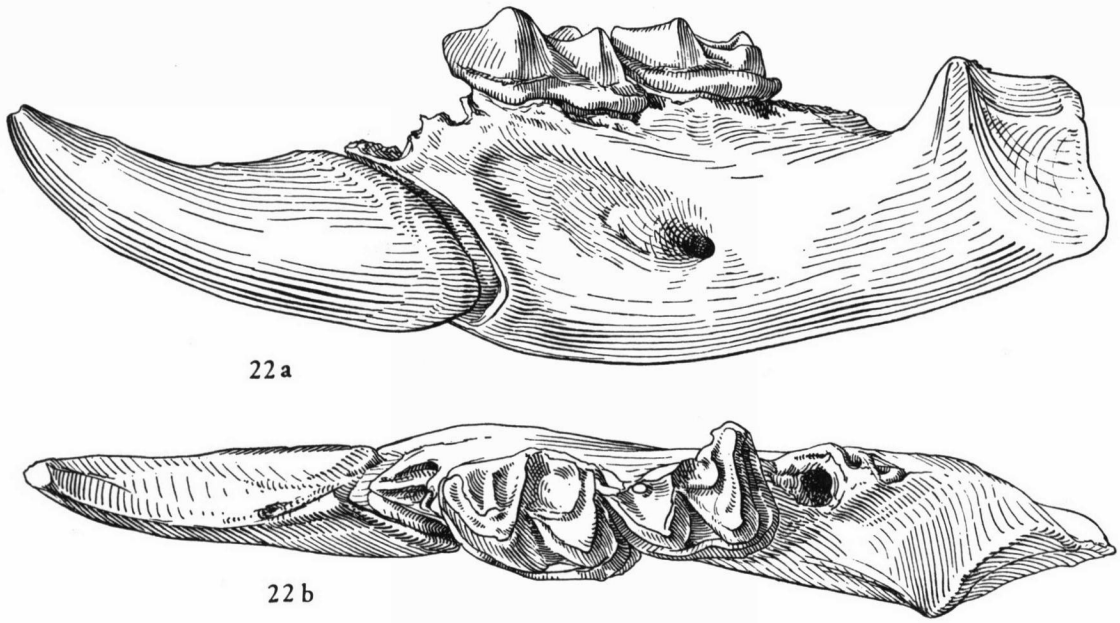



FIGURE 22. *Heterosorex roperi,* ×11. Left ramus with $\overline{I}$, $M_1$, and incomplete $M_2$, KU10030; 22a, lateral view 22b, occlusal view.

*sorex* so far as I know. It overlaps the incisor in normal soricid fashion, and it has one large anterior cusp. The posterior part of the tooth is deeply incised for the premolar (or premolars). Of these teeth in *H. sansaniensis* (interpreted from their alveoli) GAILLARD (1915, p. 86) says that the anterior tooth was much larger than that following; the alveolus of the latter is much reduced, its anteroposterior diameter measuring scarcely a third of that of the preceding alveolus. [But this is not evident to me in my study of the specimen concerned.] PATTERSON & MCGREW do not directly mention the relative size of the alveoli in *Domnina,* but by inference they may be equal.

In *Heterosorex roperi,* the teeth posterior to $\overline{C}$ (or $P_1$) and anterior to the molars are known only by their alveoli. One might expect only a single tooth by analogy with *H. sanseniensis*, but the cavity or cavities present are too complex to really be open to this interpretation, and I suspect that possibly as many as three teeth (as in *Domnina*) lay behind the $\overline{C}$. Three of my specimens, KU10027, KU10029, KU10030, taken together offer evidence leading to a tentative determination of the lower dental formula. Immediately adjacent to the $\overline{C}$ is a small, shallow pit that may have borne a premolar. Behind it is a much larger pit that in KU10029 and KU10030 is only partly divided by slight septal extensions of the alveolar wall into a shallower socket in front and a deeper depression behind. In KU10027, the two are separate. There are then four alveoli, and possibly four teeth between the $\overline{I}$ and $M_1$, and certainly more than two. If a two-rooted premolar was present a smaller number of teeth would be present. Such double-rooted teeth are known in certain Miocene shrews, but none has been described in species of *Heterosorex*. In KU10027, the third alveolus from the incisor contains what appears to be either a fragment of a tooth or a complete, platelike tooth in a vestigial state. If this is a complete tooth, $P_4$ was single-rooted. If the maximum number were present, agreement with *Domnina* is reached except that the $\overline{C}$ is distinctly larger than any of the three posterior teeth; in *Domnina* $\overline{C}$ and $P_4$ are distinctly larger than $P_1$-$P_2$. At best in *H. roperi* $P_4$ is only moderately larger than $P_1$-$P_2$. Since the figure of *H.* aff. *neumayrianus* by VIRET & ZAPFE (1951, p. 425, fig. 12) shows for $P_4$ an alveolus that is long anteroposteriorly, four (instead of the three reported) teeth may have been present—if $P_4$ was not two-rooted at that stage.

In the Basel collections (Natural History Museum) a specimen of *H. sansaniensis,* Ss 887, seem to show at least one more tooth than is usually reported for that species. Ss 887 is almost identical in alveolar pattern with KU10029 except that what is merely an incomplete septum between $P_4$ and the preceding premolar becomes a wall at depth in ours. It is possible also to compare the alveoli of KU10029 with KU10027 and KU10030, and conclude that the differences among them result from breakage: Specimens KU10027 and KU10030 compared by themselves alone to Ss 887, however, suggest that *H. roperi* had one more tooth than the Sansan specimen. An additional tooth also seems to be present in the upper jaw.

In any case, consistently or as individuals, *H. sansaniensis* almost surely had one more tooth than authors have thought. Possibly it agreed with *H. roperi* in dental formula. Perhaps the best speculation, however, is that *H. roperi* had four teeth and *H. sansaniensis* three teeth intervening between incisors and molars. I suspect from an examination of Ss 887 that the alveolar walls were incomplete naturally whereas ours normally had complete walls. Moreover, *H. roperi* probably had a slightly longer antemolar-postincisor alveolar area. These differences would be in accord with presumed differences in geologic age.

*Domnina,* however, can hardy be directly ancestral to the Oligocene species of *Heterosorex* if SCOTT (1894) has reported correctly the reduction of the zygomatic arch beyond the condition reached by *Heterosorex* in the late Miocene. These speculations on the antemolar teeth may be summarized as follows: (1) Oligocene——*Domnina* and *Heterosorex* aff. *neumayrianus,* C-$P_4$ present, $\overline{C}$ and $P_4$ much larger than $P_1$-$P_2$ in *Domnina,* and at least $\overline{C}$, $P_1$, and $P_4$ present in *H.* aff. *neumayrianus;* (2) Early Miocene——*Heterosorex roperi,* $\overline{C}$, $P_1$, $P_2$, $P_4$ present, $\overline{C}$ much larger than $P_1$-$P_4$; (3) Late Miocene——*H. sansaniensis,* $\overline{C}$, $P_4$, and at least one additional premolar present, $\overline{C}$ much larger than $P_4$.

The lower molars decrease in size from $M_1$ to $M_3$. Generally speaking, they differ from those of *Domnina gradata* in that (1) the paraconid of $M_1$ is blunter, less knifelike, and perhaps less distinctly set off from the protocone; (2) the post-entoconid valley separating that cusp from the posterior cingulum is absent (a very unshrew-like character); (3) the heel of $M_3$ is less reduced and has a much greater development of the entoconid; (4) the metaconid is more nearly equal to the protoconid in elevation; (5) the outer cusps are less V-shaped, and (6) the metaconid is slightly more posterior in position relative to the protoconid. These same features, except possibly the last, serve to separate *Heterosorex roperi* from *Blarina* and in the lower molars *Domnina gradata* is more nearly like *Blarina* than is *Heterosorex*. The lower molars of the European species of *Hetersorex* seem to be entirely comparable to those of *H. roperi.* In the holotype of *H. delphinensis* (La Grive) the heel of $M_3$ appears to be nearly if not quite unicuspid, and hence narrower than in *H. roperi.* Sansan specimens may also generally speaking have narrower heels on $M_3$ but in Ss 603 (Basel collections) the heel of $M_3$ is clearly bicuspid and quite like that in some of

our specimens—KU10008 (the holotype specimen) for example.

*Measurements of* Heterosorex, *in Millimeters*

| | *H. roperi* | *H. sansaniensis* |
|---|---|---|
| $I^2$, tr | 1.3-1.6 | ..... |
| $I^3$, ap | 1.8-2.0 | ..... |
| tr | 1.5-1.6 | ..... |
| $\underline{C}$ ap | 1.0 | ..... |
| tr | 1.0 | ..... |
| $P^3$, ap | 1.0(a) | ..... |
| tr | 0.9(a) | ..... |
| $P^4$, ap | 2.0-2.1 | ..... |
| tr | 2.0±2.2 | ..... |
| $M^1$-$M^3$, ap | 5.0 | 5.0 |
| $M^1$, ap | 2.0-2.1 | 2.0 |
| tr | 2.5 | 2.0 |
| $M^2$, ap | 1.8-2.3 | 2.0 |
| tr | 2.3-2.7 | 2.0 |
| $M^3$, ap | 1.2 | 1.0 |
| tr | 1.7 | 1.5 |
| $\underline{I}_1$ tr | 1.3-1.5 | ..... |
| $\underline{C}$(or $P_1$), ap | 1.5 | ..... |
| tr | 1.3 | ..... |
| $M_1$, ap | 2.1-2.6 | 2.2 |
| tr | 1.5-2.0 | ..... |
| $M_2$, ap | 1.75-2.1 | 1.9 |
| tr | 1.3-1.7 | ..... |
| $M_3$, ap | 1.5-1.8 | 1.7 |
| tr | 1.2-1.5 | ..... |
| $M_1$-$M_3$, ap | 5.1-5.9 | 5.8 (5.2-6.0) |
| $M_3$ length (b) | 6.0 | ..... |
| $M_1$ depth(c) | 2.8(d)-3.1 | ..... |

(a) Measured along alveolar line, tooth oblique; such measurements perhaps misleading.

(b) Length posterior edge of incisor alveolus to posterior edge of $M_3$ alveolus.

(c) Depth of jaw beneath $M_1$.

(d) Estimated.

*Relationships.* Among species of *Heterosorex*,[5] *H. roperi* is distinctly larger than *H. neumayrianus,* ($M_1$-$M_3$ ap diameter, 4.5 mm.) and differs from *H. sansaniensis* in almost certainly having a different dental formula as well as in several other particulars previously discussed. The Colorado species seems less specialized than the Vindobonian and Sarmation *H. sansaniensis* and is perhaps more advanced than the Aquitanian species, *H. neumayrianus*; the Colorado species for example is larger, but its greater specialization cannot be demonstrated at present. Indeed, premolar reduction may be more advanced in the European species.

Notice should be given, also, to *Domnina compressa,* a new species described by *Galbreath* (1953, p. 46) from the Oligocene of Colorado. That species exhibits several features characteristic of *Heterosorex:* (1) elongate depression anterior to mental foramen; (2) more convex inferior border of ramus than in *D. gradata;* (3) larger talonid of $M_3$, entoconid present; (4) better union of entoconid to hypoconid than in *D. gradata;* (5) less union of entoconid to metaconid; (6) more acute angle of incisor in jaw; (7) overlap of molar teeth; (8) slightly posterior position of metaconid relative to protoconid; and (9) more nearly equal height of molar cusps, exclusive of protoconid. On the other hand, GALBREATH states that the beginning of the intertemporal fossa can be made out in his specimen. [The same statement was made by PATTERSON & MCGREW (1937) in their study of *D. gradata.*] If this fossa were present, then *D.* compressa could not be reassigned to *Heterosorex* which otherwise seems a very distinct possibility. I suspect that a real intertemporal fossa is not present in *D. compressa* (a slight depression exists in *H. roperi,* and the fossa is not present in *D. thompsoni*), and that the species should be referred to *Heterosorex.* If *compressa* is a species of *Heterosorex,* the interesting problem is raised as to whether two lines of descent, dating from the Oligocene, are represented, or only repeated migration between the New World and the Old World. To a lesser extent, this same problem is present in *Plesiosorex* (with *Metacodon*) and in *Plesiosminthus* among rodents.

*Heterosorex roperi* is clearly a species of *Heterosorex* rather than of *Domnina.*[6] This is shown, for example, by what is preserved of the zygomatic arch (more complete in *H. roperi*); the less reduced heel on $M_3$; and the lack of separation of the entoconid from the posterior cingulum of the lower molars. The first two are features in which the Oligocene *Domnina* is already more specialized than the Martin Canyon species. Possibly *Domnina* is ancestral to *Blarina.* PATTERSON & MCGREW (1937, p. 255) were inclined to view with caution the apparent relationship of *Domnina* to *Blarina* because of the supposed existence of Miocene species of the living genera of shrews. This they took to indicate that the differentiation "of the family into groups now surviving may have taken place as early as the Oligocene, if not earlier." But some of these records do not so well support this view as one might suppose. Thus, STIRTON (1930, p. 222, after VIRET) says of *Sorex antiquus,* distinguished from the common shrew "only by a slight difference in the form of the ascending ramus and by a little smaller size", but STEHLIN (1940, p. 300, fig. 1) has figured a jaw of this species which shows two extra premolar

[5] An unnamed species of *Heterosorex* is recorded in the Flint Hills Miocene by MACDONALD (1951, p. 72).

[6] GALBREATH (1953, p. 92) was certainly mistaken in supposing that the fragments he described, which do pertain to a single genus and species, were those of an unnamed genus. The lack of fluorescence has been shown not to be decisive in fossil material. Such parts as GALBREATH had, which are represented by comparable parts in *Heterosorex,* are identical.

teeth in the lower jaw. *Heterosorex,* however, has been placed in a separate subfamily, *Heterosoricinae,* by VIRET & ZAPFE (1951). Still, *Blarina, Heterosorex,* and *Domnina* have features which suggest a real relationship, and it is obvious that we need much more material than we have at present in order to more than speculate on the evolution of the shrews. It is clear that *Heterosorex* represents an aberrant line. As now described, *Domnina* (type species) seems not to be ancestral to *Heterosorex,* although close in many ways to what the structural ancestor presumably was like. I think it is highly probable, however, that the series *Domnina thompsoni* (without intertemporal fossa), *D. compressa,* and *Heterosorex roperi* is an approximate phylogenetic series, as in essence GALBREATH (1953, p. 49) has previously suggested. More complete specimens of *Domnina* are needed to show the presence or absence of an intertemporal fossa in any species of *Domnina,* and possibly a restudy of the zygomatic region in *Domnina gradata* is pertinent to ascertain the degree of completeness of the arch. [SCOTT's statement that it was incomplete was based on a specimen now lost.]

#### HETEROSOREX? sp.

Assigned to the genus *Heterosorex,* with varying degrees of certainty, are three specimens that have in common a somewhat smaller size than is shown by specimens assigned to *Heterosorex roperi.* These are: a jaw fragment with right $M_1$-$M_2$ (KU10035); a jaw fragment with left $M^1$-$M^2$ (KU10036); and a jaw fragment with broken right lower incisor and four alveoli behind (KU10034). Measurements of KU10035, followed by those in parentheses for the smallest specimen (KU10027) of *H. roperi* are given in millimeters as follows: $M_1$, ap. 1.8(2.1), tr. 1.5(1.7); $M_2$, ap. 1.8 (1.8), tr. 1.3 (1.5). Visual comparison leaves an impression of distinctly smaller size that is not altogether conveyed by the measurements. Differences other than in size are less apparent. The metaconids of KU10035 seem to be more rounded pillars, and the basins of the trigonids and talonids may be more nearly closed at the inner margins.

The incisor of KU10034 seems to be smaller than those of specimens allocated to *H. roperi.* If that specimen is to be referred to *Heterosorex,* the presence of four alveoli behind the incisor, seemingly for the antemolar dentition, almost certainly demonstrates that the maximum dental formula suggested for *H. roperi* was indeed present. The transverse width of the incisor of KU10034 is almost as large as that doubtfully recorded for the largest specimen (KU10043) of *Sorex vireti.* Direct visual comparison, however, serves to separate even this specimen of *S. vireti* from KU10034.

The most divergent of the three specimens in respect to individuals of *Heterosorex roperi* is KU10036. It like the others is somewhat smaller, although only slightly, and somewhat differently proportioned in $M^1$-$M^2$ as well. More important differences are, in KU10036: (a) inner cusps more anteroposteriorly compressed into crescents, (b) conules (protoconule and metaconule) present, (c) mesostyle divided, and (d) ectoloph seemingly to be less developed in relation to inner half of tooth.

*Measurement of Specimen KU10036 and* Heterosorex roperi

| | KU10036 | *H. roperi* |
|---|---|---|
| $M^1$, ap | 2.0 | 2.0-2.1 |
| tr | 2.5 | 2.5 |
| $M^2$, ap | 1.8 | 1.8-2.3 |
| tr | 2.2 | 2.3-2.7 |

It obviously cannot be demonstrated that the three specimens, KU10034-KU10036, pertain to a single species. They do all, however, seem to be related to *H. roperi.* They might in fact be extreme variants of this species although I do not think so. The differences cited seem to warrant tentative separate recognition, but the incomplete character of the specimens deters me from proposing a new name.

### Subfamily SORICINAE

Two species of shrews closely related to living shrews are found in the Martin Canyon fauna. Both are here referred to the existing genus *Sorex,* but it is doubtful that either these, or comparable species in the Miocene of Europe, truly represent this genus. The assignment to *Sorex* is made to emphasize the relation of our two species to European ones now assigned to *Sorex,* rather than to suggest necessarily a closer relationship to *Sorex* than to some other extant genera of shrews.

#### SOREX VIRETI Wilson, n.sp.

Figures 23-28

This species is named in honor of Professor JEAN VIRET, of Lyon, France, for his distinguished work on fossil Insectivora.

*Holotype.* Right lower jaw bearing $M_1$-$M_3$, No. 10037, Univ. Kansas Mus. Nat. Hist.

*Referred specimens.* KU70038, upper incisor; KU 10039, $M^3$; KU10040-KU10043, lower incisors; KU10044, KU10045, KU10046-KU10048, KU10049, lower jaws.

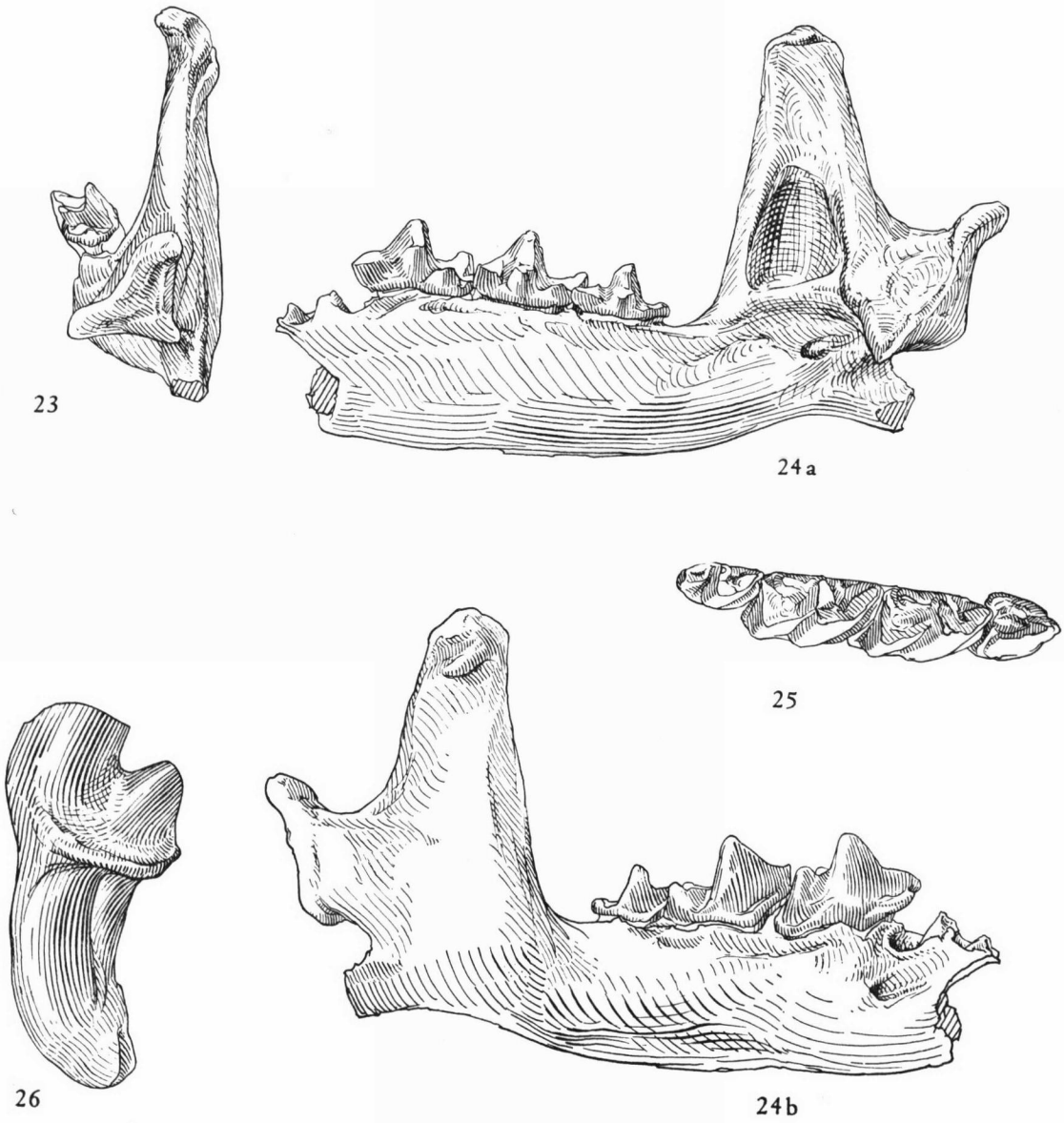
*Geological age and locality.* Sandy silts of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Diagnosis.* A species of *Sorex* larger than *S. grivensis,* and approximately the size of *S. dehmi,* but perhaps slightly larger. Mental foramen under anterior part of $M_1$ at end of a depression. Dental foramen beneath midline of intertemporal fossa, which is relatively low

and long anteroposteriorly. Dental formula possibly $\overline{1,1,2,3}$. Single rooted $P_4$; heel of $M_3$ single-cusped, but with small basin.

*Description.* Upper jaw parts are seemingly restricted to a broken incisor, and a third molar. The principal cusp is broken off the upper incisor. A large basal cusp is present that in the state of wear present is essentially bicuspid. This incisor seems to conform generally to the type seen in Recent *Sorex,* but the basal caspule is perpendicular to the posterior border of the crown rather than essentially parallel as in *Sorex* and *Crocidura.* I presume this indicates a more oblique insertion into the premaxillary bone. The third upper molar is not notably different from that figured by VIRET & ZAPFE (1951, p. 414, fig. 3) for *S. grivensis* (Vindobonian).

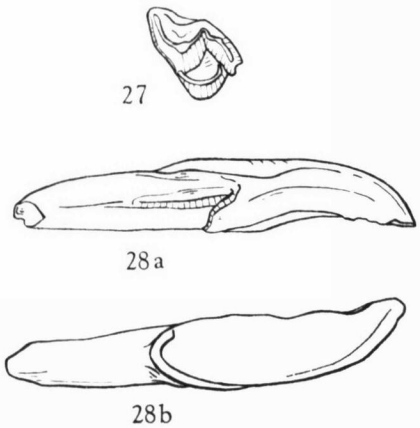
None of the lower jaws assigned to *Sorex vireti* has the incisor present. Four isolated lower incisors in the collections from Quarry A have been assigned to *S. vireti.* Even the smallest one seems too large to pertain to *S. compressus* although measurements show one incisor to be larger than the rest. The upper margin of these teeth, when not too much worn, show in addition to the tip, two low but well-marked crenulations as in *S. grivensis* and *S. antiquus* (Aquitanian), but not so




FIGURES 23-26. *Sorex vireti.*————23, Posterior view of right ramus, KU10047.————24, Type specimen, right ramus with $M_1$-$M_3$, KU10037; 24a, medial view; 24b, external view.————25, Occlusal view of right $P_4$-$M_3$, KU10044.————26, Lateral view of incomplete right $I^2$, KU10038. [Fig. 26, ×18; all others ×11.]

well-marked as in *S. antiquus* VIRET & ZAPFE, 1951, fig. 1; STEHLIN, 1940, figs. 1b, 3). There is a small basal cuspule.

The only antemolar preserved is $P_4$ in KU10044. It is not so compressed when viewed laterally as is $P_4$ of *S. compressus*. The principal cusp is only slightly higher than the paraconid of $M_1$. Two ridges lead posteriorly from the cusp; the external one is the stronger and occupies a nearly median position on the crown; the other, fainter



FIGURES 27, 28. *Sorex vireti*, all ×9.5.————27, Occlusal view of left $M^3$, KU10039.————28, Right $\bar{I}$, KU-10040; 28a, superior view; 28b, lateral view.

one, follows the internal border of the tooth. The emphasis on the external ridge in $P_4$ of *S. vireti* suggests a beginning stage in the evolution of the type seen in the living *Sorex* in which the external ridge is V-shaped, resembling the external V of the trigonid of the molars. A delicate cingulum is present. The tooth is single-rooted in contrast to the two-rooted condition in *S. compressus* and *S. dehmi* (Vindobonian) (VIRET & ZAPFE, 1951, p. 415).

In the molars, the talonid of $M_1$ is not noticeably widened; in this respect it is more nearly like that of *S. grivensis* or *S. antiquus* than like that of *S. dehmi*. The tooth is only slightly larger than $M_2$. $M_3$ is distinctly smaller, has a single-cusped heel that nevertheless is slightly basined and that supports an external ridge occupying a median position and an internal ridge extending forward to the trigonid. This tooth is more reduced, and more unicuspid than in *S. grivensis*. Entoconids are prominent on all molars, and separate from the posterior cingula. External cingula are absent or extremely delicate on all molars. This last seemingly corresponds to the condition in *S. antiquus* rather than that in *S. grivensis* or *S. dehmi*.

The dental formula for the lower dentition of *Sorex vireti* is unknown. Only two rami, KU10037 and KU10049, have the alveoli at all preserved. The specimen KU10037 suggests $\frac{1\,1.2.3}{}$, as the most likely formula. The presence of the additional vestigial premolar cannot be clearly established but the configuration of the socket of the canine suggests it. A toothless lower jaw, KU10049, seems to pertain to *S. vireti*. If so, it almost certainly confirms a dental formula of an enlarged incisor and three additional antemolar teeth. The formula as given agrees with the stage of antemolar reduction seen in *S. grivensis* rather than the dentition of *S. dehmi* or the older *S. antiquus*.

In the lower jaw the mental foramen is placed slightly more to the rear than in any other Miocene species of *Sorex* to which I have been able to compare it. In *S. vireti*, the foramen is under the anterior part of $M_1$ at the end of a shallow depression, rather than under the posterior part of $P_4$ as in *S. grivensis* or under the middle part of $P_4$ as in *S. antiquus* or under the anterior part of $P_4$ as in *S. dehmi*. The root for the enlarged incisor terminates beneath the posterior root of $M_1$. The intertemporal fossa is large, triangular, and has a somewhat rounded apex, but is notably less high than in *S. compressus*. In proportions the fossa resembles that of *S. dehmi* rather than that of *S. antiquus* or *S. grivensis*, and the dental foramen, as in *S. dehmi*, is well under the fossa rather than at its posterior margin. The condyle is like that of the various Miocene shrews referred to *Sorex*. It does not, however, really have a double articulation although tending strongly in that direction in the possession of a complex articular face.

**SOREX COMPRESSUS Wilson, n.sp.**

Figures 29-31

*Holotype.* Fragment of left lower jaw bearing $P_4$-$M_2$, No. 10050, Univ. Kansas, Mus. Nat. Hist.

*Referred specimens.* KU10051, upper jaw bearing $P^3$-$M^2$; KU10052, KU10053, KU10054-10057, lower jaws.

*Geologic age and locality.* Sandy silts of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

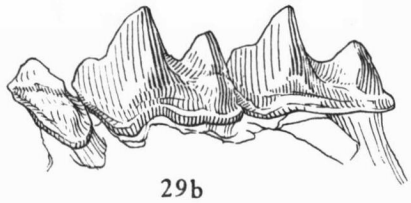
*Diagnosis.* A species of *Sorex* approximately the size of *S. antiquus*. Mental foramen under root of $P_4$ and anterior part of $M_1$, at end of a depression. Dental foramen beneath mid-line of intertemporal fossa, which is relatively high and short anteroposteriorly. Enamel colored?. Dental formula not known. Double-rooted $P_4$, the crown of which is compressed as seen in lateral view; metaconid of $M_1$ closely appressed to protoconid; apex of $P_4$ about on level with paraconid of $M_1$.

*Description.* The upper dentition is better known in *Sorex compressus* than in *S. vireti* for KU10031 in our collections is a left upper jaw bearing $P^3$-$M^2$. $P^3$ is a minute tooth with a low simple crown on a single root. $P^4$-$M^2$ agree with comparable teeth of *S. grivensis* except in: (1) parastyle and protocone of $P^4$, especially the former, less developed, (2) hypocones of $M^1$ and $M^2$ less projecting, protocones more crescentic, (3) $P^4$ perhaps less angulate in outline. The same distinctions seem to

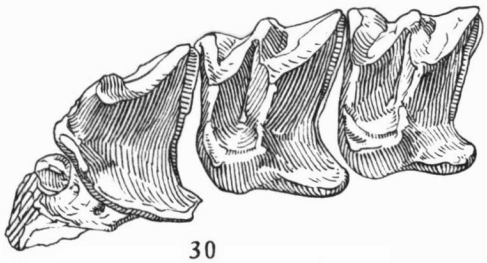
hold true in comparison with *S. antiquus* except that the outline of $P^4$ may be more as in this Aquitanian species. The differences cited also separate, even more sharply, the existing *S. araneus*. A little of the side of the skull is preserved in KU10051 and this shows the infraorbital foramen and orbit to be comparable in structure and in topographic relationship to the dentition to those structures in *S. grivensis*.

Of the lower jaw and dentition, nothing is known in *Sorex compressus* anterior to $P_4$. In one specimen or another, however, the structure of $P_4$-$M_3$ and of the jaw posterior to $P_4$ is reasonably well revealed.

29a



29b



30

FIGURES 29, 30. *Sorex compressus.*————29, Type specimen, left ramus with $P_4$-$M_2$, KU10050; 29a, occlusal view; 29b, lateral view.————30, Occlusal view of left $P^3$-$M^2$, KU10051. [Figs. 29a, 29b, ×18; Fig. 30, ×17.]

The fourth lower premolar is slender when viewed laterally—more so than in *S. antiquus*, which has the next most slender $P_4$ of any Miocene species. $P_4$ seemingly possesses two roots as does *S. dehmi*. $P_4$ possibly is unlike that of both *antiquus* and *dehmi* in that the tip does not rise appreciably above the paraconid of $M_1$. However, the tip does not rise appreciably above in Sg 842 (Lyon Coll.) that has been labeled *S. antiquus*.

The first and second molars seem to have the same relative proportions to each other as in *S. vireti*, but those of *S. compressus* are relatively shorter anteroposteriorly. $M_3$ seems less reduced. The external cingula are weak or lacking as in *S. vireti*.

In $M_1$, the metaconid is closely appressed to the protoconid, probably more so in *S. dehmi* than in any of the other Miocene species of *"Sorex"*, although Sg 842 *(S. antiquus)* is similar. The relation of the metaconid and protoconid closely resembles that in the genus *Limnoecus* STIRTON (1930). The heel of $M_3$ is too worn in the one known specimen for comment as to its structure.

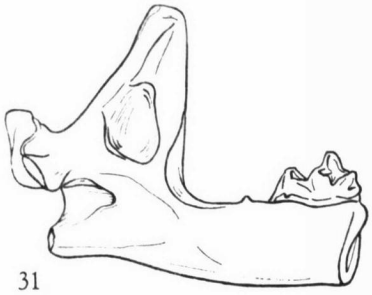
*Measurements of* Sorex, *in Millimeters*

| | *vireti* | *compressus* | *grivensis* | *antiquus* | *dehmi* |
|---|---|---|---|---|---|
| $I^2$, ap | 1.5? | ..... | ..... | ..... | ..... |
| tr | 0.9? | ..... | ..... | ..... | ..... |
| $P^4$-$M^2$, ap | ..... | 3.4 | 4.2 | 3.86+ | ..... |
| $P^4$, ap | ..... | 1.2 | ..... | ..... | ..... |
| tr | ..... | 1.4 | ..... | ..... | ..... |
| $M^1$, ap | ..... | 1.1 | ..... | ..... | ..... |
| tr | ..... | 1.5 | ..... | ..... | ..... |
| $M^2$, ap | ..... | 1.0+ | ..... | ..... | ..... |
| tr | ..... | 1.4 | ..... | ..... | ..... |
| $M^3$, ap | 1.0— | ..... | ..... | ..... | ..... |
| tr | 1.6 | ..... | ..... | ..... | ..... |
| $\bar{I}$, tr | 0.75-1.0? | ..... | ..... | ..... | ..... |
| $P_4$-$M_2$, ap | 4.1 | 3.0 | ..... | ..... | ..... |
| $M_1$-$M_2$, ap | 3.1-3.25 | 2.25-2.5 | ..... | ..... | ..... |
| $M_1$-$M_3$, ap | 4.1+-4.25 | 3.2+ | 3.5-3.6 | 3.25 | 3.8-4.0 |
| $P_4$, ap | 1.2 | 0.6— | ..... | ..... | ..... |
| tr | 1.0 | 0.6 | ..... | ..... | ..... |
| $M_1$, ap | 1.7-1.8— | 1.2 | ..... | ..... | ..... |
| tr | 1.1-1.25 | 0.9 | ..... | ..... | ..... |
| $M_2$, ap | 1.5-1.7 | 1.0+-1.1+ | ..... | ..... | ..... |
| tr | 1.0-1.1 | 0.8 | ..... | ..... | ..... |
| $M_3$, ap | 1.2-1.3 | 1.0 | ..... | ..... | ..... |
| tr | 0.7+-0.9 | 0.6 | ..... | ..... | ..... |
| $M_3$ to I(a) | 5.3 | ..... | ..... | ..... | ..... |

(a) Length, posterior border of $M_3$ to posterior border of $\bar{I}$.

The mental foramen of the lower jaw is at the end of a depression, and beneath the posterior part (and root) of $P_4$ and the anterior part of $M_1$, the two teeth overlapping to this extent. The rear of the lower jaw and the position of the dental foramen are quite like those of *S. vireti*. The condyle is close in configuration to that of *S. vireti*, but perhaps with a greater convexity of surfaces, and a more ventral rather than posterior position to the lower part of the condyle. The most striking difference between the two American species lies in the distinctly higher and narrower intertemporal fossa

of *S. compressus*; thus it resembles *S. grivensis* rather than *S. dehmi*.[7]



31

FIGURE 31. *Sorex compressus*, ×9.5. Medial view of left ramus with $M_2$, KU10053.

#### COMPARISONS

Only four genera of soricids have been reported from the Miocene of the World. These are *Heterosorex, Limnoecus, Crocidura,* and *Sorex* (SIMPSON, 1945).[8] Of these, *Heterosorex* is remote in affinities to the other genera, and to *S. vireti* and *S. compressus*. I am not sure of the Miocene record of *Crocidura*; perhaps it was based only on *Crocidura schlosseri,* now regarded as a synonym of *Heterosorex sansaniensis*. Recently BUTLER & HOPWOOD (1954) have identified a fragmentary lower jaw from the Miocene of Kenya as *Crocidura* sp. indet. In any case, the late Miocene *Limnoecus* (represented by the type, *L. tricuspis* (STIRTON, 1930), and *L. niobrarensis* (MACDONALD, 1947) is said to be close to *Crocidura*. The species referred to *Sorex* can be regarded as pertaining to that genus only in a loose sense (VIRET & ZAPFE, 1951) and seem to be no more closely related to *Sorex* than *L. tricuspis* and *L. niobrarensis* are to *Crocidura*. A pecularity of this record up to now is that only crocidurine shrews were known from the Miocene of North America, a place where they do not now live, and only soricine (red-toothed) shrews from the Old World.

Differences between the new species and those previously recognized and named can best be put in tabular form. *Sorex gracilidens* of the Vindobonian (VIRET & ZAPFE, 1951, p. 417) is so distinct that it is omitted from consideration. Seemingly, no types or topotypes of *S. desnoyerianus* or of *S. prevostianus* still exist, and those two species are also excluded. Judging from written descriptions, they are distinct from the American species. In addition to those tabulated, other differences exist, which further distinguish the several species, but those presented in the table indicate sufficiently the specific validity of *S. vireti* and *S. compressus* and convey an impression not only of the synthetic quality of the various species but also of the broad nature of the generic assignments of European species to *Sorex*.

VIRET & ZAPFE (1951, p. 414) state that characters in *Sorex grivensis* demonstrate that the separation of shrews into those with pigmented teeth and bicuspid heel (Soricinae) and unpigmented teeth and unicuspid heel (Crocidurinae) can not be applied to the fossil species. Some students of Recent mammals have also questioned the separation for living shrews.

If the various species assigned by VIRET & ZAPFE to *Sorex* are to be placed in a single broad genus for convenience in our present state of ignorance of shrew phylogeny, then *S. compressus* and *S. vireti* can be so assigned also for the differences between *S. gracilidens, S. dehmi,* and *S. grivensis* are greater than those separating the American species from *S. antiquus* or *S. grivensis*. At the same time possible assignment to *Limnoecus* should be held in mind. *S. vireti* may be considered in this regard. It undoubtedly has features which are (1) primitive, although being primitive may favor one living shrew rather than another without necessarily any special affinity, or (2) specialized, even if we are uncertain which are the specialized features. We can not be sure of either category although separation is critical for a determination of relationships. *S. vireti* resembles *Crocidura* in the following features: (1) a relatively complex, but still technically single condyle; (2) a single heel cusp on $M_3$; (3) lack of prominent serrations on $\bar{I}$; (4) large triangular intertemporal fossa; and (5) protoconid and metaconid of $M_1$ close together.

*S. vireti* more nearly resembles *Sorex* in (1) structure of $P_4$; (2) more quadrate, less wedge-shaped $M_1$ and $M_2$; (3) somewhat better development of post-entoconid valley of $M_1$ and of $M_2$; and (4) crown height.

The resemblance to *Limnoecus,* and especially *L. niobrarensis,* is greater than to *Crocidura,* and the resemblance to Miocene species of *Sorex* is, of course, much greater than to *S. araneus*. It should also be stressed that *S. vireti* is older geologically than either of the two species of *Limnoecus* which are late Miocene, and also that both species of *Limnoecus* are specialized in $M_3$ to a point which prevents them from being re-

[7] Considerable variation is present in the specimens assigned to *Sorex grivensis,* as for example in the shape of the intertemporal fossa and the structure of $P_4$. Whether this variation is real within the population of *S. grivensis* or is the result of maintaining original determinations after additional species had been recognized in the Miocene of Europe, I do not know.

[8] GREEN (1956) has described and named a new genus and species of insectivore, *Domninoides riparensis,* from the early Pliocene (Clarendonian) of South Dakota. At the same time he wrote of a lower Rosebud (Arikareean) species of the genus that differs only in lesser development of the cingula. GREEN assigned *Domninoides* to the Soricidae and compared his new genus with *Domnina*. Judging from GREEN's figures and descriptions, *S. vireti* and *S. compressus* are not closely related to *Domninoides*. In my view, *Domninoides* is a talpid rather than a soricid.

*Comparisons of* Soricidae

| Character | *Sorex vireti* | *Sorex compressus* | *Sorex antiquus* | *Sorex grivensis* | *Sorex dehmi* | *Limnoecus niobrarensis* | *Limnoecus tricuspis* |
|---|---|---|---|---|---|---|---|
| 1. Dental formula | $\overline{1'\ 1'\ 2^{?},\ 3}$ | Unknown | $\overline{1'\ 1'\ 3',\ 3}$ | $\overline{1'\ 1'\ 2',\ 3}$ | $\overline{1'\ 1'\ 3',\ 3}$ | $\overline{1'\ 1'\ 1',\ 3}$ | $\overline{1'\ 1'\ 1',\ 3}$ |
| 2. Position of mental foramen | Anterior part of $M_1$, at end of depression | Beneath posterior part (and root) of $P_4$ and anterior part of $M_1$, at end of depression | Under middle of $P_4$ | Under posterior part of $P_4$ in depression | Under anterior root of $P_4$ in depression | ??? | ??? |
| 3. Character of $P_4$ | Not notably compressed in lateral view, apex not especially higher than paraconid of $M_1$ | Compressed in lateral view, apex subequal in elevation to paraconid of $M_1$ | Relatively compressed in lateral view, slightly higher than paraconid of $M_1$ | Not compressed in lateral view, apex not appreciably higher than paraconid of $M_1$ | Not compressed in lateral view, apex notably higher than paraconid of $M_1$, two-rooted | Not compressed in lateral view, apex subequal with paraconid of $M_1$ | Not compressed in lateral view, apex overtops paraconid of $M_1$ |
| 4. Position of dental foramen | Well under intertemporal fossa | Well under intertemporal fossa | More posterior in position | More posterior in position | Well under intertemporal fossa | Well under intertemporal fossa | Posteriorly placed (as figured) |
| 5. Heel of $M_3$ | Reduced to single cusp, but basined | Unknown | Moderately developed, but unicuspid | Moderately developed, but unicuspid | Reduced with single cusp, but basined | Single trenchant cusp, but moderately large | Unicuspid, (also no metaconid) |
| 6. Talonid of $M_1$ | Not appreciably widened | Not appreciably widened | Not appreciably widened | Not appreciably widened | Appreciably widened | Not appreciably widened | Appreciably widened |
| 7. Pigmentation | Absent? | Present? | Present | Absent | Absent? | Absent | Absent? |
| 8. Shape of intertemporal fossa | Relatively low and broad | Relatively high and narrow | Relatively high and narrow | Relatively high and narrow | Relatively low and broad | Relatively low and broad | Relatively high and narrow (as figured) |
| 9. $M_1$-$M_3$, length | 4.1+-4.25 | 3.2+ | 3.25 | 3.5-3.6 | 3.8-4.0 | 3.1 | ??? |

garded as directly ancestral to living species of *Crocidura.* It may be supposed that in the above list of resemblances to *Crocidura,* features 1, 3, and 4 are primitive, and that in the list of resemblances to *Sorex,* features 2, 3? and 4 are likewise primitive.

Thus only the structure of $P_4$, which suggests the beginning of a specialization not seen in *Crocidura,* prevents *S. vireti* from being regarded as a primitive crocidurine. Figures and descriptions of *Limnoecus* are inadequate to permit comparisons, but $P_4$ of *L. tricuspis* at least probably is not of the *S. vireti type.* Features 2 and 5 in which *S. vireti* resembles *Crocidura* are noteworthy resemblances also to *Limnoecus.* In actual fact, however, 2 and 5 can be found in such species as *Sorex dehmi* as well.

It is possible to speculate: (1) the modern genera and probably even several of the suprageneric groups of shrews are of post-Miocene development; (2) the *Crocidura-Sorex* groups of species were not clearly differentiated in Miocene times; and (3) pigmentation having once been acquired—possibly all shrews possessed this character at one time in the past—it has been lost sporadically in various groups, and has quite limited phylogenetic implications.

The assignment of *S. vireti* to *Sorex* is made to emphasize the many resemblances to European species, and in the same sense that various species of early squirrels are referred to *Sciurus. Sorex compressus* may be referred to *Sorex* for the same reasons. In the close approximation of protoconid and metaconid it resembles *Limnoecus,* but also *S. dehmi,* and in several ways it is more nearly like *Sorex* than *Crocidura.*

## Family TALPIDAE

### Subfamily SCALOPINAE

So far as can be ascertained, only representatives of the subfamily Scalopinae (SIMPSON, 1945, p. 52) are present at Quarry A. Certainly no members of the Talpinae are to be recorded.

### Genus MYDECODON Wilson, n.gen.

Figures 32-33

*Type species. Mydecodon martini* WILSON, n.sp.

*Diagnosis.* Small ($M_1$-$M_3$=4.2 mm.) shrewlike moles with dental formula: $?\ \overline{2.1.3.3}$. $\overline{C}$ small, $P_1$ (?) absent, $P_2$ single-rooted, $P_3$-$P_4$ double-rooted, $P_2$-$P_4$ graded in size, largest posteriorly. Molars with moderately brachydont crowns, external cingula present, anterior arms of hypoconids reaching to the bases of metaconids, talonid valleys somewhat basined in consequence of entoconid and metaconid ridges. Trigonid cusps of $M_1$ crowded together. Two mental foramina in lower jaw, one under anterior root of $P_4$, the other beneath anterior part of $M_1$.

#### MYDECODON MARTINI Wilson, n.sp.

This species is named in memory of Handel T. Martin, one of the first to collect fossil vertebrates in the vicinity of Quarry A.

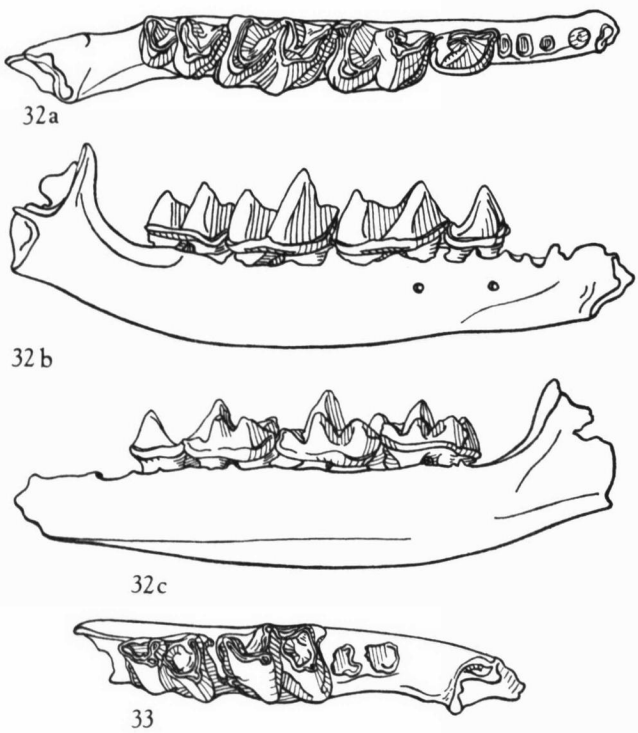
*Holotype.* Incomplete right lower jaw, No. 10058, Univ. Kansas Mus. Nat. Hist., with $\overline{C}$, $P_4$-$M_3$ and alveoli for remaining teeth.

*Referred specimens.* Fragmentary lower jaws, KU-10059-KU10066.

*Geological age and locality.* Sandy silts of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Diagnosis.* Only one species known. Characters same as given for the genus.

*Description. Mydecodon martini* is a mole of shrew-like size, being somewhat smaller than *Urotrichus talpoides*. No certainly referable upper teeth or skeletal parts are known. The most completely preserved specimen is the type, but the absence of some teeth in it leaves uncertainty as to the dental formula. Prolonged




FIGURES 32, 33. *Mydecodon martini,* all ×9.5.——— 32, Type specimen, KU10058, right ramus with $P_4$-$M_3$; 32a, occlusal view; 32b, lateral view; 32c, medial view. ———33, Occlusal view of left ramus with $M_1$-$M_2$, KU10062.

study of the specimens has suggested to me that the dental formula may well be that seen in *Dymecodon pilorostris*. Of the critical I-Pm series only two teeth are present—one certainly $P_4$, the other probably that called the canine in *Dymecodon*. Alveolar sockets are present for at least four more teeth, which I think to be the maximum number present. The most anterior alveolus, obviously for an incisor, is a moderate-sized, slanted socket. Behind this is a somewhat less slanting hole also of good size for the supposed second incisor. Next comes $\overline{C}$ which occupies a more upright socket, but still slanting, of about the size of that for the posterior incisor. The crown of $\overline{C}$ (now broken off and lost) although projecting forward with the single root to the rear is of premolariform rather than caniniform shape. The socket for the canine is deep and slightly larger than that for the following premolar. In addition to the principal cusps there is a tiny one on the heel. $P_2$ is known only by its alveolus. This alveolus is slightly smaller than that of $\overline{C}$ and more vertical although the anterior wall is somewhat inclined. $P_3$ has two essentially vertical sockets which together have an anteroposterior diameter nearly equal to that of $P_4$. $P_4$ is a single, relatively broad tooth having a slight external cingulum in addition to the principal cusp and heel. Wear prevents any detailed description of the heel area.

Other alternatives to the above interpretation are possible, but I think only one is likely. It is that $P_2$-$P_3$ are single-rooted, and that $P_1$ is represented by the socket here assigned to $P_2$. The alveoli ascribed to $P_3$ are spaced nearly as in $P_4$ rather than being smaller as one would expect. Further, the teeth in fossil insectivores are loose in the jaws and frequently drop out before recovery. Few sockets are occupied by the roots of otherwise missing teeth. In KU10060 the alveolus immediately anterior to $P_4$ has a root in it, but the one in front does not. The crown may have been broken off, possibly in the course of recovering the specimen, in which case it is easier to visualize a single-rooted $P_3$ than a double-rooted one. Nevertheless direct comparison of the dentition with those of *Dymecodon pilorostris* and *Urotrichus talpoides* convinces me that $P_3$ was double-rooted. If the dental formula for *Dymecodon* is $\frac{2.1.3.3}{}$, as usually given, the remainder of my interpretation is a necessary accompaniment except for the possibility of an additional incisor. I have three jaws, each with anterior alveoli. They all have the same number of alveoli, and this together with the similarity in dental pattern and sizes of molars to those of *Urotrichus, Uropsilus,* and *Dymecodon* suggest a reduced number of incisors as in those genera.

In connection with the dental formulae of the living Japanese "shrew-moles," study of the lower dentitions of *Mydecodon, Dymecodon,* and *Urotrichus* suggests to me that possibly the dental formula of the two genera named first is $\frac{1.1.4.3}{}$. This change would bring into agreement the incisor formulae of all the small shrewlike moles *(Uropsilus, Nasillus, Neurotrichus, Urotrichus,* and *Dymecodon).*

The lower molars are moderate in their crown height, and agree generally with those of *Dymecodon* except that the protoconid is less elevated relative to other

molar cusps as in that genus. They bear small, but distinct, external cingula that are continuous except where interrupted in some specimens on the lateral margins of the protoconids. $M_2$ is the largest molar, but $M_1$ is not much smaller, and $M_3$, although the smallest, is a robust tooth. The dimensions of $M_1$ and $M_2$ overlap, as between individuals. A characteristic of all three molars is the tendency for the talonid valley to be basined as a consequence of the fore- and aft-extensions of the metaconid and entoconid cusps. The anterior arms of the hypoconids do not rise to the tips of the metaconids, but end against their bases.

The first molar is a wedge-shaped tooth in the pointed anterior half of which the trigonid cusps, especially the metaconid and protoconid, are crowded together. A cingulum surrounds the tooth except on the inner side. Posterointernally this cingulum is expanded into a triangular projection. The anterior arm of the hypoconid does not, in this tooth, reach the metaconid but ends against the base of the protoconid on its internal edge. The paraconid is distinctly the lowest cusp of the five making up the crown. The protoconid is slightly the highest cusp, and metaconid, entoconid, and hypoconid are all nearly equal.

$M_2$ has the talonid and trigonid widths nearly equal and is more nearly rectangular in outline than $M_1$. The posterointernal expansion of the cingulum into a triangle is less pronounced, and may possibly be absent in individual cases. The trigonid cusps are farther apart, and the anterior arm of the hypoconid reaches to the base of the metaconid. The heel cusps, entoconid and hypoconid, are relatively lower than in $M_1$.

In $M_3$ the talonid is narrower than the trigonid. As in that of $M_2$, it is relatively lower than in $M_1$. The posterior cingulum persists as a very obscure ledge.

The jaw of *Mydecodon martini* is not well enough preserved to warrant extended comment. It seems to resemble that of *Urotrichus* except in longer and slimmer anterior part in relation to less reduced anterior dentition. Of the two mental foramina present, the anterior one lies beneath the anterior root of $P_4$; the other is beneath the anterior part of $M_1$. In the posterior position of the anterior foramen, *Mydecodon martini* shows closer resemblance to *Uropsilus* than to *Urotrichus* or *Dymecodon*.

Several upper molars in the collection from Quarry A have patterns one might expect for *Mydecodon,* that is, like those in *Urotrichus* and *Dymecodon,* and thus not like those of *Uropsilus*. These teeth seem, nevertheless, too large for allocation to *Mydecodon,* and seemingly are to be associated with *Scalopoides,* also from Quarry A.

Various humeri of moles from Quarry A could be associated with *Mydecodon* on basis of size. Judging from associations maintained by authors for material from the Oligocene-Miocene of Europe, these humeri are slightly too large to belong to *Mydecodon*. They seem also to be too fossorial to pertain to a mole related to *Dymecodon* or *Urotrichus,* and are much too specialized to pertain to an uropsiline mole. Lack of humeri of a size to be assigned to *Mydecodon* may indicate that the humerus is relatively little specialized, and has escaped notice in the large quantities of still unsorted limb bones from Quarry A.

*Measurements of* Mydecodon martini *and* Mygatalpa avernensis, *in Millimeters*

| | *Mydecodon martini* | *Mygatalpa avernensis* |
|---|---|---|
| C-$M_3$, ap | 6.6 | ..... |
| $P_2$-$M_3$, alveolar | 5.8 | ..... |
| $M_1$-$M_3$, ap | 4.2 | 4.2-4.5 |
| Depth (inside) of jaw beneath $M_1$ | 1.4 | 1.4 |
| C, ap | 0.7 | ..... |
| tr | 0.5 | ..... |
| $P_4$, ap | 0.9-1.0 | 1.0 |
| tr | 0.7 | 0.6 |
| $M_1$, ap | 1.3-1.5 | 1.5 |
| tr | 1.0-1.1 | 1.05 |
| $M_2$, ap | 1.5-1.6 | 1.65-1.7 |
| tr | 1.0+-1.1 | 1.05 |
| $M_3$, ap | 1.3 | 1.25 |
| tr | 0.9-0.9+ | 0.80 |

*Relationships.* There seems to be no mole of this kind and size previously described from the Miocene of North America. In Europe several Miocene species or specimens have been described within the size range of *Mydecodon martini,* and agreeing with it in some other characters, as well as one from the upper Stampian (Oligocene). These may be listed as follows: (1) *Mygatalpa avernensis* [*Talpa cfr. brachychir,* VIRET], $M_1$-$M_3$=4.2-4.5 mm., Upper Stampian, Coderet-Bransat, Chauffours, and Marcoin; (2) *Talpa brachychir,* $M_1$-$M_3$ =4.2-4.8 mm., late Aquitanian, Weisenau, Haslach bei Ulm; (3) *Scaptonyx edwardsi,* $M_1$-$M_3$=4.5 mm. and 5.2 mm., Vindobonian, La Grive St. Alban, Neudorf; (4) Undetermined talpids I and II of ZAPFE, $M_1$-$M_3$= 3.7?, $M_1$-$M_2$=3.1, Helvetian, Neudorf; (5) Undet. talpid, SEEMAN, $M_1$-$M_3$=4.5 mm., Sarmatian, Viehhausen.

All except the last three have presumptively associated jaws and humeri, but the type specimen is in each case a humerus. This is an awkward point in comparing an American species which lacks an associated humerus. In any case, the American species does not belong to either *Talpa* or *Scaptonyx,* even in a broad sense.

The genus *Mygatalpa,* with *Mygale avernensis* POMEL as type, was established by A. SCHREUDER (1940, p. 320-324) for a collection of fragments of jaws, isolated teeth, and humeri from several different Oligocene localities of France. The lower jaw material although of earlier age than ours has a close resemblance in size (see measurements), and such morphological features as can be seen from the figures or are described by SCHREUDER. $P_4$-$M_3$ of *Mydecodon* differs so far as descrip-

tions and figures can carry one in: (1) $M_2$ with less compressed trigonid (distance between paraconid and metaconid greater); (2) internal trigonid valley of $M_2$ deeper between metaconid and paraconid; (3) cingulum of $M_2$ not passing around paraconid to base of metaconid but ending at anterointernal corner of tooth; (4) external cingulum of $M_2$ a trifle stronger; and (5) talonid of $M_3$ slightly shorter.

Anterior to $P_4$, the alveoli of the premolars are known in one specimen of *Mygatalpa*. VIRET (1929, p. 45-46) has interpreted these alveoli as pertaining to $P_1$-$P_3$ with the posterior two premolars being double-rooted. This is in contrast with our species where $P_2$, at least, is single-rooted, but it seems possible to me, after examination of the specimen, that $P_2$ could be single-rooted as in ours. The alveoli of *Mygatalpa* are described by SCHREUDER as standing rather vertically. The corresponding anterior two in ours are rather slanted, but the relative degree of slanting would be difficult to prove.

The differences cited above although perhaps minor are, under the circumstances, best taken as suggesting a species with a comparable molar construction—possibly as a result of a relatively primitive construction—but sufficiently unlike to be regarded as generically distinct.

SCHLOSSER's figures (1888, pl. 3) of the jaw of *Talpa brachychir* are not sufficiently detailed to permit comparison with our specimens. In his description (p. 132), he merely compares the jaw to that of *Talpa*. In any case, the type material consists of three humeri.

*Scaptonyx edwardsi* is probably slightly (La Grive St. Alban) or even considerably larger (Neudorf, ZAPFE, 1951) than our species. $P_2$-$P_3$ are double-rooted. It is not beyond possibility that *Mydecodon* is related to one or another of the fossil species of small moles now assigned to *Scaptonyx*.

The undetermined talpid of SEEMANN (1938) has been compared with *Mygatalpa* by SCHREUDER (1940). The former, like *S. edwardsi,* seems to be a slightly larger mole than *Mydecodon martini*. $P_2$-$P_3$ are both single-rooted. $P_2$ is described as incisiform rather than premolariform. In *M. martini* $\overline{C}$ (or $P_1$?) is premolariform, and presumably the more posterior teeth, including the missing $P_2$, would also be premolariform rather than incisiform. Of the two undetermined talpids of ZAPFE (1951), II is a talpine obviously unrelated to *Mydecodon*. Talpid I, as figured by ZAPFE, has a $P_4$ with a small metaconid lacking in *Mydecodon,* a ridged metaconid in $M_2$ which closes the trigonid valley to the inside, and an additional alveolus in the lower jaw.

North American Miocene talpids known by something other than humeri include only *Proscalops secundus* (lower Miocene), *Domninoides,* unnamed species (lower Miocene), and *Talpa incerta* of the lower Snake Creek (upper Miocene). The last named species is based on a fragmentary jaw with $M_3$. It is said to have shorter teeth than either *Proscalops* or *Proscapanus* (MATTHEW, 1924, p. 74). *P. secundus* is considerably larger than *M. martini*. *Proscalops* seems to be represented at Quarry A by several isolated teeth (see later pages of this work) which in their crown height and compression of the protoconids and hypoconids are notably unlike *M. martini*. $P_3$ in *Proscalops* is single-rooted. *Domninoides* (GREEN, 1956, p. 152-154) is much larger than *Mydecodon* with double-rooted $P_2$; $P_2$-$P_3$ is set transversely in the jaw; the hypoconid arms of the molars are longer; $M_2$-$M_3$ talonid valleys open freely to the inside; and the posterior mental foramen is under the posterior root of $P_4$. Nevertheless, if GREEN is correct in his determination of the number and character of the teeth—$\frac{1.0.4.3}{}$ with incisor enlarged—a relationship to such genera as *Mydecodon, Dymecodon,* and *Urotrichus* is suggested. GREEN, of course, referred *Domninoides* to the Soricidae. The following characters of *Domninoides*, however, are consonant with an assignment to the Talpidae, and in most of them opposed to an assignment to the Soricidae: (1) antemolars five in all, $P_2$-$P_4$ double-rooted; (2) diastema between $P_3$ and $P_4$; (3) triangular enlargement of posterior cingula in $M_1$ and $M_2$; (4) extension of anterior crests of hypoconids to corresponding metaconids; (5) lack of a postentoconid valley in molars; (6) wide heel of $M_3$ unreduced, bicuspid; and (7) no fluorescence in molars (absence of pigmentation).

Among Recent moles, *Mydecodon* seems to have resemblances to the *Uropsilus* group, the *Urotrichus* group, and *Scaptonyx*. *Scaptonyx,* however, has a premolar series unlike that of *Mydecodon*. $P_4$-$P_2$ are graded as to size with $P_3$-$P_4$ two-rooted, $P_2$ one-rooted. $P_1$ is distinctly larger than $P_2$ and, moreover, two-rooted. There is a slight diastema in front of $P_1$ (into which space the upper canine projects?). The canine or $I_3$ is absent, the dental formula probably being: $\frac{2.1.4.3}{}$. Although it is customary to place *Scaptonyx* in the Scalopinae, the specialization of $P_1$ is talpine, even though this tooth is not enlarged to the extent seen in typical talpines. An enlarged $P_1$ and incisiform $\overline{C}$ is developed in certain artiodactyls such as the oreodonts and hypertragulids, and there this transformation has been regarded as of considerable taxonomic importance (e.g., SCOTT, 1940, and as applied to moles, SCHLOSSER, 1887, p. 128). Perhaps the position of *Scaptonyx* among moles should be reinvestigated. *Scaptonyx jaegeri* (SEEMANN, 1938, p. 20) (the only fossil species of *Scaptonyx* with the anterior dentition well preserved) does not show this specialization at all. I would consider it doubtful that *S. jaegeri* is really to be assigned to *Scaptonyx*.

Of the other two groups mentioned, the Uropsilinae and the *Urotrichus* group *(Urotrichus, Dymecodon),* it is hardly possible in the absence of both the upper dentition and the humerus to state to which *Mydecodon* shows the closest affinities.

From *Dymecodon* the Quarry A genus differs in: (1) less elevated protoconid of molars relative to other molar cusps; (2) trigonid cusps of $M_1$ slightly more crowded together; (3) external cingula better developed, especially $M_1$; (4) anterior mental foramen more posterior in position; (5) $\underline{P}_3$ double-rooted rather than single-rooted; and (6) $\overline{C}$ slightly more robust in *M. martini*.

From *Uropsilus* the American genus differs in: (1) slightly more extended anterior arms of hypoconids of lower molars; and (2) basining of the talonid valleys by development of anteroposterior extensions of the metaconid and entoconid cusps.

On the above tally, *Mydecodon* shows closer resemblance to *Uropsilus* than to *Dymecodon*. My impression, nevertheless, is that the American genus is more closely related to *Dymecodon* as the name itself, an anagram, suggests. If the upper molars referred to the genus next to be discussed were after all those of *Mydecodon*, the resemblance to *Uropsilus* would be much less. If the humeri, also assigned to this other genus, were to be referred to *Mydecodon*, reference to the Uropsilinae would be beyond consideration. It is not, however, on these possibilities that my impression is based, but on the character (see comparison above) of the talonid valleys. A similar feature is seen in *Mygatalpa*, and also in the supposedly unrelated *S. edwardsi*, *S. jaegeri* and *Scalopoides isodens* (Quarry A). It can hardly be taken as a sure guide to special relationship where it exists, but its presence in several genera distinct from the uropsiline group gives one the feeling that *Mydecodon* is likewise in a different branch of the Talpidae.

## Genus SCALOPOIDES Wilson, n.gen.

Figures 34-39

*Type species. Scalopoides isodens* WILSON, n.sp.

*Diagnosis.* Scalopine mole of dental formula: ? $\frac{3.1.4.3}{}$. Incisors and canine small, $P_1$ small, incisiform?. $P_2$ single-rooted, $P_3$-$P_4$ double-rooted. Molar crowns more or less mesodont, protoconids and hypoconids angulate, prominent metastylids present on flanks of metaconids in $M_2$-$M_3$, anterior arms of hypoconids reaching to bases of metaconids, entoconids extended anteriorly to help enclose elongate talonid valleys internally. $M_1$-$M_2$ subequal. $M_3$ smaller but robust. Lower jaw decidedly talpid in shape. Two mental foramina, one beneath posterior root of $P_4$ or more usually beneath space between $P_4$ and $M_1$, and the other beneath posterior root of $P_3$. Upper molars tritubercular with hypocones obscure or absent, conules obscure or absent.

### SCALOPOIDES ISODENS Wilson, n.sp.

*Holotype.* Left lower jaw with $I_3$-$P_1$, $P_4$-$M_2$, No. 10067, Univ. Kansas Mus. Nat. Hist.

*Referred specimens.* Isolated upper molars KU10068-KU10070, fragmentary lower jaws, KU10071-KU10078. Isolated lower molar KU10079.

*Geological age and locality.* Silty sands of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Diagnosis.* Only known species of the genus. See generic diagnosis.

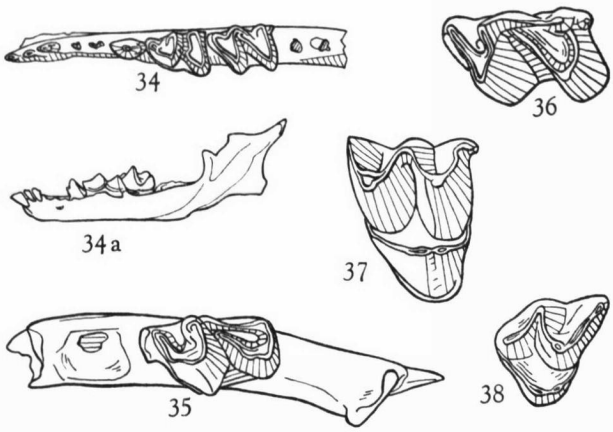
*Description.* The dental formula is probably complete, but may lack one premolar. In what possibly is a related genus, the Vindobonian *Proscapanus*, it is complete, but at one stage in my study of *Scalopoides*, I had tentatively determined the formula as $\frac{3.1.3.3}{}$. What is $P_1$ with a complete formula, I thought to be the canine, the canine $I_3$ and so forth. This other formula may yet prove to be the correct one, which is more in line with a relationship to *Neurotrichus*, but in jaws of *Proscapanus sansaniensis* available for comparison, $P_1$ seems slightly caniniform, and its alveolus is a forwardly slanting hole. The bottom of this socket is slightly external to the other premolar alveoli. All these features suggest a socket for the canine just as I had supposed was the case in *Scalopoides*, but in *Proscapanus* it can be demonstrated to be otherwise. Consequently, I am describing the anterior dentition as if the formula were known to be complete.[9]

Only one specimen has any of the anterior dentition preserved or for that matter much of the jaw, and that is the type, KU10067. In it the alveolus for $I_2$ is partly preserved. Nothing really can be made out except that there is no reason to believe the tooth itself was notably different in size from that of $I_3$-$\overline{C}$. The following incisors and canine are preserved and are not unlike $I_2$-$I_3$ of *Talpa*. $I_3$ is larger than $\overline{C}$. The $P_1$ is somewhat larger than $\overline{C}$, but smaller than $I_3$. It seems incisiform to me.

Following the first premolar, and not separated from it by an appreciable diastema, is the alveolus for the single-rooted $P_2$. This alveolus is of good size and may have been occupied by a relatively robust tooth. The anterior edge of the alveolus is slanting, however, and this suggests that there was no space between $P_2$ and $P_1$ (into which an enlarged upper canine might intrude if my first supposition regarding the identity of these teeth was correct). The typical talpine specialization seems to be lacking then in the anterior dentition regardless of how the dental formula is interpreted. $P_3$ is represented only by its alveolus, but this shows a two-rooted condi-

[9] ELLERMAN & MORRISON-SCOTT (1951, p. 29-34) have stressed the taxonomically unreliable nature of the anterior dentition in moles. Although I think these authors have seriously overextended their arguments, they have cited data that obviously suggest the need for caution in basing taxonomic assignments on the mere presence or absence of one or another of the anterior teeth. I do not think interpretation of the relationship of *Scalopoides* would need be much altered by the presence or absence of $P_2$, for example.

tion to be present with the anterior socket considerably narrower transversely than the posterior one. The roots of the premolars, then, show a progressive reduction toward the front, and this may have been true of the crowns as well. The combined sockets of $P_3$, however, are not greatly different in size from those of $P_2$.




FIGURES 34-38. *Scalopoides isodens.*————34, Type specimen, left ramus with $I_3$-$P_1$, $P_4$-$M_2$, KU10067; 34a, lateral view; 34b, occlusal view.————35, Occlusal view of left ramus with $M_3$, KU10071.————36, Occlusal view of left $M_2$, KU10073.————37, Occlusal view of right $M^2$, KU10068.————38, Occlusal view of right $M^3$, KU10070. [Fig. 34a, approximately ×3; Fig. 34b, ×4.5; all others ×9.5.]

$P_4$ is represented by the tooth in the type jaw. A rather weak external cingulum is present that is expanded at the anterior edge of the crown of the tooth and forms a small basal cuspule. The tip of the principal cusp is situated about one-third the way back from the anterior margin of the crown, and a ridge leads down the posterior surface of the cusp to the area of the short heel. The posterior surface of the principal cusp and the external surface of the heel is somewhat excavated. There is a small heel cusp present. The principal cusp as well as the accessory ridge and cuspules tend to be lined up with the inner cusps of the molars, and hence to occupy a relatively internal position on the crown of $P_4$. KU10042 had a corroded tooth in advance of $M_1$ which must also be a $P_4$ but because of its poor preservation is not included in the table of measurements. As it is now preserved, 10042 is smaller than 10067.

The molars are all of good size, and $M_1$-$M_2$ are nearly equal although the second molar is slightly the larger. Their crowns have acquired some height, and can be described as mesodont. They resemble *Mydecodon* in structure but differ as follows: (1) in $M_1$, (a) outer cusps are relatively higher in respect to inner, possibly reflecting increased hypsodonty, (b) trigonid cusps are more widely separated, (c) the anterior arm of the hypoconid is slightly more extended internally, and (d) the hypoconid is more angulate; (2) in $M_2$, (a) the protoconid and hypoconid are more angulate, (b) the paraconid is closer to the metaconid, (c) a strong metastylid occurs on flanks of the metaconid, which with wear nearly but not quite unites with the anterior arm of the hypoconid; (3) in $M_3$, (a) the heel is relatively longer, and (b) other differences are found as in (2); and (4), generally (a) the talonid basins are more obliquely compressed so as to become almost trenchlike, and (b) the anterior cingulum in $M_2$-$M_3$ tends to expand at the base of the paraconid, and the triangular expansion of the posterior cingulum in $M_1$-$M_2$ is somewhat less pronounced.

The lower jaw is not well enough preserved for much comparison, but it is markedly talpid in character. The anterior mental foramen is beneath the posterior part of $P_3$; a somewhat smaller posterior mental foramen is either beneath the space between $P_4$ and $M_1$, or beneath the posterior root of $P_4$. The jaw is notably similar to that of *Neurotrichus* save for the more anterior position of the posterior foramen.

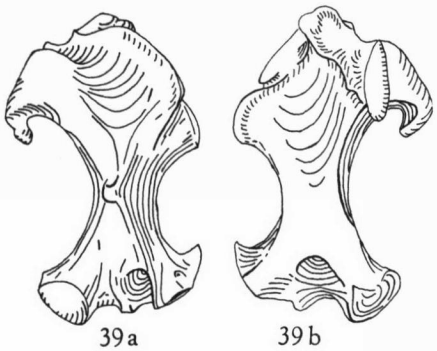
Judging from the relative sizes of upper and lower molars of several species of living moles, three tuberclular upper molars pertaining to a rather primitive mole probably should be assigned to *Scalopoides isodens.* KU10068 is an $M^2$. The anterior cingulum is absent except for a small parastyle. The posterior cingulum is faint but expanded into a minute metastyle. No division of the mesostyle can be seen. A small, and faint, protoconule lies close to the protocone. No trace of a metaconule can be made out, and the hypocone is exceedingly obscure, but the latter may be represented by a slight bulge in the posterior crest of the protocone. This tooth is close to Cod. 2134 in the collections of the Natural History Museum at Basel assigned by SCHREUDER to *Mygatalpa* and to molars at Lyon as well. Differences are to be observed (Quarry A specimens may be higher crowned, for example), but these hardly seem to be greater than those that separate one fossil species from another of the same genus. KU10069 and KU10070 are third upper molars. In these a cingulum is absent, but a small parastyle is present. The metacone is not crescentic as it is in $M^2$. Again a small protoconule located close to the protocone can be discerned. Bulges on the posterior crest of the protocone in one specimen could be said to be vestigial metaconule and hypocone. Even these traces are absent in the second specimen. A slight division of the mesostyle can be seen on one specimen but not on the other. These teeth are also close to one referred to *Mygatalpa* by SCHREUDER (Basel Museum, Bst 5024). Upper molars of *Proscapanus sansaniensis,* so far as I can determine, have never been adequately figured. They

seem to have the same general construction as those from Quarry A, but to be somewhat higher crowned.

*Measurements of* Scalopoides isodens, *in Millimeters*

| | | | | |
|---|---|---|---|---|
| $Pm_2$-$M_3$, alveolar | | | 8.4 | |
| $M_1$-$M_3$, alveolar | | | 5.3-5.8 | |
| Depth of jaw beneath $M_1$ (inside) | | | 2.0 | |
| $P_4$, ap | 1.3 | $M_1$, ap | | 1.9-2.0+ |
| tr | 0.9 | tr | | 1.5—1.5 |
| $M_2$, ap | 2.0+-2.3 | $M_3$, ap | | 2.0 |
| tr | 1.4-1.6 | tr | | 1.2 |

Eleven humeri or parts of humeri are clearly to be assigned to a talpid in a moderate stage of fossorial specialization. These are KU10080-KU10090. In view of the several moles occurring in the Quarry A collections, it might be expected that the humeri would not pertain to a single kind of mole. Nevertheless, with some allowance for growth stage and a certain amount of postmortem abrasion in some of the specimens, it is not possible to separate these humeri. Probably they do represent a single species. If this is so, then to which one of the several kinds do they belong? There is sufficient variation in living moles in size of front legs in relation to size of dentition (nearly the only way of associating my specimens) to permit more than one of the several fossil species to be associated with the humeri. By far the most probable association, however, is association with *Scalopoides isodens* as shown by the following discussion.



39a 39b

FIGURE 39. *Scalopoides isodens,* ×4. 39, Right humerus, KU10082; 39a, anterior view; 39b, posterior view.

The Quarry A specimens have the following dimensions in millimeters: length, 10.0-10.4; breadth of distal end, 5.0-6.0; breadth of proximal end, 6.25-6.6; breadth of shaft, 2.0-2.4+; depth (ap) of shaft, 2.0- to 2.3. Several specimens are somewhat damaged. The three best-preserved specimens measure in millimeters: length, 10.0-10.4; breadth at distal end, 5.3-5.5+; breadth at proximal end, 6.25-6.6; breadth of shaft, 2.2-2.4+; depth of shaft, 2.1-2.3.

The proximal heads of the humeri are wider than the distal heads, and the shafts are nearly equidimensional; this last-mentioned feature is unusual. The teres tubercle is less developed than in such an advanced mole as *Talpa,* although it merges with the head much more than in such kinds as belong to *Urotrichus* or *Scaptonyx.* The recess under the great tuberosity is, moreover, not so deep as in *Talpa.* CAMPBELL (1939, p. 16) describes as a character of the Scalopinae a sharp crest "running from the medial side of the scapular facet to the distal end of the lesser tuberosity." This crest is extremely powerful in British Museum specimens of *P. sansaniensis.* In *S. isodens* it is present, but rather weakly developed. It is seemingly not greatly different in respect to this crest from some specimens of *Talpa* or of *"Talpa" minuta.* CAMPBELL, however, did not include *Neurotrichus* in the Scalopinae. The pectoral crest is less pronounced than in *Urotrichus,* and the angle of its distal descent is less acute. The length-breadth proportions which are a measure of the degree of fossorial specialization serve to place these humeri at about the level of specialization seen in humeri of *Condylura,* and at a less specialized level than humeri of *Talpa* or *Scapanus,* but more specialized than the humeri of *Scaptonyx, Urotrichus,* and *Neurotrichus.* Humeri of *S. isodens,* in addition to proportions, agree except for minor details with those of *Condylura.* A simple measure of degree of specialization, which has been employed in the past, is the ratio of length to greatest breadth (whether distal or proximal). For present purposes this ratio seems sufficient. Data from various published sources, together with some that are original, show the relative degree of specialization of the Quarry A humeri given in the following tabulation.

*Ratio of Length to Greatest Breadth of Humerus in Various Talpids*

| | |
|---|---|
| 1.07 | *Scapanus latimanus,* Recent |
| 1.33 | *Talpa europea,* Recent |
| 1.35-1.40 | *Talpa? minuta,* Miocene, La Grive St. Alban, Neudorf |
| 1.42-1.51 | *Talpa meyeri,* Miocene, Weissenau bei Mainz |
| 1.45-1.47 | *Proscapanus sansaniensis,* Miocene, La Grive St. Alban |
| 1.51-1.61 | Quarry A specimens |
| 1.54 | *Condylura cristata,* Recent |
| 1.63 (a) | *Mygatalpa avernensis,* Oligocene, Coderet |
| 1.76-1.83 | *Scaptonyx jaegeri,* Miocene, Viehhausen |
| 1.81 | *Scaptonyx edwardsi,* Miocene, La Grive, Neudorf |
| 1.89 (b) | *Mygatalpa avernensis,* Oligocene, Coderet |
| 1.94 | *Urotrichus talpoides,* Recent |
| ?1.94 | *Neurotrichus gibbsii,* Recent |
| 2.02 | *Scaptonyx dolichochir,* Miocene, La Grive |
| 2.74 | *Sorex trowbridgii,* Recent |

(a) Based on length of about 8 mm. as given by VIRET, 1929.
(b) Based on length of 9.3? (same specimen) as given by SCHREUDER, 1940.

It may be noted also that those above the Quarry A specimens (that is, less than 1.51) have broader proximal than distal ends; in those below, the reverse situation holds. All the small "shrew-moles" also fall below the Quarry A specimens.

Although the relation of molar size to humeral length can not be a rectilinear one in all cases, it may well be so for those moles on the same general level of specialization. This seems to be the only quantitative way in which a probable association of humeri with jaws from Quarry A may be reached. The following graph (Fig. 40) takes as control points data of $M_1$-$M_3$ length and humeral length based on one Oligocene and three Miocene species of moles that have humeri bracketing in degree of specialization those of Quarry A. It should be noted, however, that only with the Viehhausen material is there undoubted association of molars and humeri. A straight line drawn through these control points intersects the 10.0-10.4 mm. spread of the humeri of Quarry A to give $M_1$-$M_3$ lengths agreeing best with *Scalopoides*.

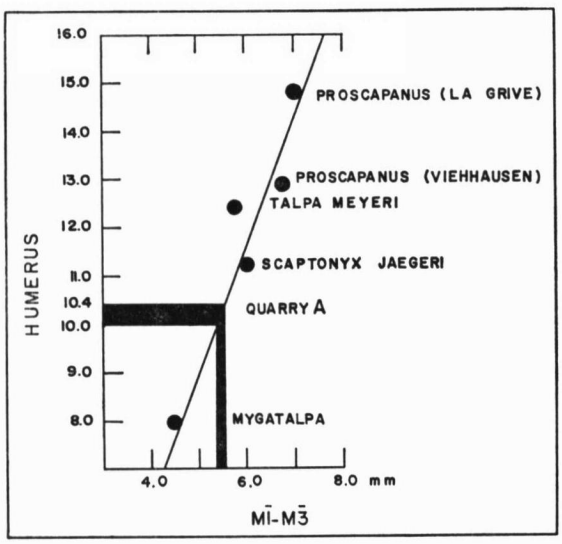



FIGURE 40. Graph of ratio of length of humerus to length of lower molar series for *Scalopoides isodens,* and for one Oligocene and three other Miocene species of moles. [$M_1$-$M_3$, length: Quarry A. *Dymecodon martini:* 4.1-4.4 (composite of isolated teeth, otherwise 4.2). *Scalopoides isodens:* 5.9-6.3 (composite of isolated teeth, otherwise 5.3-5.8). *Proscalops?* sp.: 7.1 (estimate based on isolated $M_1$-$M_2$ only). *Proscalops* sp., cf. *P. secundus:* 8.8-9.3 (composite of isolated teeth).]

Seemingly much too large to be associated with these humeri is material identified as cf. *Proscalops secundus. Proscalops,* also from Quarry A, is rare and one would hardly expect such a large number of humeri to pertain to it. *Mydecodon,* if my estimation of affinities is correct, should be associated with a humerus of the relatively unspecialized, slender type seen in *Scaptonyx* and *Urotrichus*. Perhaps the humerus of *Mydecodon* is even less specialized than those, and has been overlooked because of this lack of specialization in the sorting of the hundreds of small bones in the collection from Quarry A. Considering the length of the molars of *Scalopoides,* I would have expected its humerus to be 11 or 12 mm. long. Other than in this there are no conflicting data.

*Comparisons. Scalopoides isodens* seem to be a scalopine mole, although the dental formula of *S. isodens* remains to be determined precisely. Likewise the genus seems to be distinct from previously named moles. To avoid undue length of discussion and possible confusion, my comparisons are made on the basis of acceptance of the formula as $\frac{3.1.4.3}{}$. It should be held in mind, however, that the tooth row might well have been incomplete. If this should prove to be the case, the position of $I_2$ through $P_1$ would be shifted forward by one tooth.

*Scalopoides* is distinct from *Mydecodon* as is indicated by the difference in dental formula, incisiform rather than premolariform canine, and in various details of the molars as indicated in the description of them.

Of the other American fossil genera,[10] *Proscalops* and *Domninoides,* the Miocene species are larger than *Scalopoides isodens. Proscalops* also has a single-rooted $P_3$ in contrast to the double-rooted condition in *S. isodens,* the premolars (in middle Oligocene species of *Proscalops* at any rate) are spaced and peglike, the molars are higher crowned with more acute protoconid-hypoconid buttresses, and the anterior arm of the hypoconid reaches well up toward the tip of the metaconid. Isolated molars of *Proscalops* are present in the Quarry A collection and quite distinct in the characteristics mentioned above. The dental formula of *Domninoides,* as given by GREEN, differs from that of *Scalopoides,* $P_2$ is double-rooted, and $P_2$-$P_3$ are spaced and set obliquely in the jaw. The molars have many points in common in the two genera, but the features of $M_1$ are more like those of $M_2$ and *vice versa* in respect to the metastylid and talonid valley. Thus, the metastylid in *Scalopoides* is absent in $M_1$, but present in *Domninoides*; in $M_2$ that stylid is well-developed in *Scalopoides* but reduced in *Domninoides;* the talonid valley of $M_1$ is open in *Scalopoides* but closed in *Domninoides*; the talonid valley of $M_2$ is closed in *Scalopoides* but open in *Domninoides.* The position of the mental foramina in the lower jaw is the same in both genera.

The European Oligocene genus *Mygatalpa* shows many points of resemblance, and little which would prevent *Mygatalpa* from being regarded as ancestral to *Scalopoides,* or other scalopines. The humeri from Quarry A, if they are to be assigned to *Scalopoides* are somewhat more fossorial (and also have a somewhat different muscle-scar pattern). The initiation of the metastylids of *Scalopoides* may be in the concave metaconids mentioned by SCHREUDER (1940, p. 322), and

[10] MATTHEW'S *Talpa incerta,* a fragment of jaw with $M_3$, can hardly be identified at a generic level.

the differences in the premolars are all in the right direction (as for example, $P_2$ with roots close together, perhaps fused in *Mygatalpa;* single-rooted, but large in *Scalopoides*). The upper molars are barely to be distinguished in the two genera, the lower molars show an equivalent degree of compression of the trigonid of $M_2$, lack of it in $M_1$, and the same elongated heel on $M_3$. Although other European Oligocene genera seem to be represented at Quarry A and the separation in age and space can be no clinching argument in the present case, the composite and fragmentary nature of *Mygatalpa,* founded ultimately on a humerus, the fact that this humerus is more primitive and different in scar pattern, and that *Proscapanus sansaniensis* is closer still in molar structure all are against assigning our material, even tentatively, to *Mygatalpa.*

The European late Miocene species, *Proscapanus sansaniensis,* seems to be distinct from *Scalopoides isodens* in the clear presence of four premolars, the single-rooted character of $\overline{C}$-$P_3$ (all much alike in size), and the more specialized humerus. These differences seem sufficient for generic separation of the species from Quarry A from *Proscapanus.*

The molars of *Scalopoides isodens,* however, agree closely in all but size with specimens of *Proscapanus sansaniensis.* The molars of the former are in fact closer than to those of other scalopine insectivores at Quarry A. This is an important point even if in most attempts to classify talpids the molars have not been stressed. The jaw likewise is in fair agreement, including the position of both mental foramina. The antemolar dentition of *Scalopoides,* however, is critical, and shows some significant difference. Briefly, the anterior dentition of *P. sansaniensis* ($I_3$-$P_3$) is described correctly as consisting of single-rooted, conical, single-cusped rather thick teeth of essentially equal size and shape. Premolars $P_3$-$P_2$ from Quarry A probably would be larger than $I_1$-$\overline{C}$, although only the alveoli of the premolars are known, and the incisor and canine are overlapping teeth in which the incisors (and canine?) have chisel-shaped (with long axis anteroposterior) rather than pointed tips.

The genus *Scaptonyx* has four premolars of which $P_1$ is double-rooted and somewhat enlarged, and *Scalopoides isodens* almost certainly represents another line of talpids. I do not think it is at all established, however, that the Sarmatian Miocene *S. jaegeri* is properly referable to *Scaptonyx. S. jaegeri* has points of resemblance to *Scalopoides* (the two may agree in molar structure), but it is at least specifically distinct: for example, *S. jaegeri* has a complete dental formula and $P_2$ is double-rooted.

Unidentified, or incompletely identified, specimens in the collections at Basel and at the University of Lyon suggest that *Scalopoides* (and *Mydecodon* as well) is represented on a generic level by species in the Sansan and La Grive faunas. Molar structure is the same, but the European specimens fail to preserve the necessary anterior dentition for proof, or when this part is present show a different line of specialization. Thus a more conservative course is to minimize these similarities for the present, and not to place European species in these genera.

*Talpa meyeri* SCHLOSSER (late Aquitanian, early? Miocene, Weisenau bei Mainz) is about the size of *Scalopoides isodens,* the associated humeri are not unlike in proportions, although those of the former are larger, and some similarities in molar proportions and patterns are to be observed in the none too clear figures given by SCHLOSSER (1888, pl. 3). However, four premolars are present in *T. meyeri.* Its $P_1$ is somewhat larger than either $P_2$ or $P_3$ which are nearly equal in size. All three anterior premolars are decidedly smaller than $P_4$. A talpine feature of *T. meyeri* is the two-rooted condition of $P_1$ (SEEMANN, 1938, p. 19). *Scaptonyx edwardsi* from Neudorf is approximately the same size as *S. isodens.* The humerus is not, however, like that of *Scalopoides,* and the jaw and teeth differ somewhat.

In regard to the broader relationships of *Scalopoides,* it could be a descendant of *Mygatalpa avernensis* if this is a real genus. It could have a special relationship to *Proscapanus sansaniensis,* although probably not. Gaillard thought that *Proscapanus* was ancestral to the American living mole, *Scapanus,* and SEEMANN (1938, p. 19) concurs in this view. Our material is too removed in structure from *Scapanus* to modify or to add anything to this conclusion.

*Scalopoides* seems not to be directly ancestral to any of the genera having species now living in North America. It is closer to *Neurotrichus* and *Condylura* than to *Parascalops, Scapanus,* or *Scalopus,* but has higher-crowned cheek-teeth than *Condylura* and different antemolar specialization, and has a more advanced humerus and lower molars than *Neurotrichus.* The synthetic character of *Scalopoides* is seen in that the humerus resembles that of *Condylura*; the antemolar dentition (lower) resembles that of *Neurotrichus*; the lower molar dentition resembles those of *Condylura, Parascalops,* and *Scapanus;* and the upper molar dentition resembles those of *Neurotrichus* and *Condylura. Scalopoides* might be described as a *Condylura*-like mole with higher-crowned teeth and with antemolar dentition specialized toward *Neurotrichus,* or perhaps better as a *Neurotrichus*-like mole, somewhat more specialized in molar dentition and more fossorial than the living species. It could have been semiaquatic as well. Whatever the systematic position of the fossil genus, it probably lived in a riparian environment.

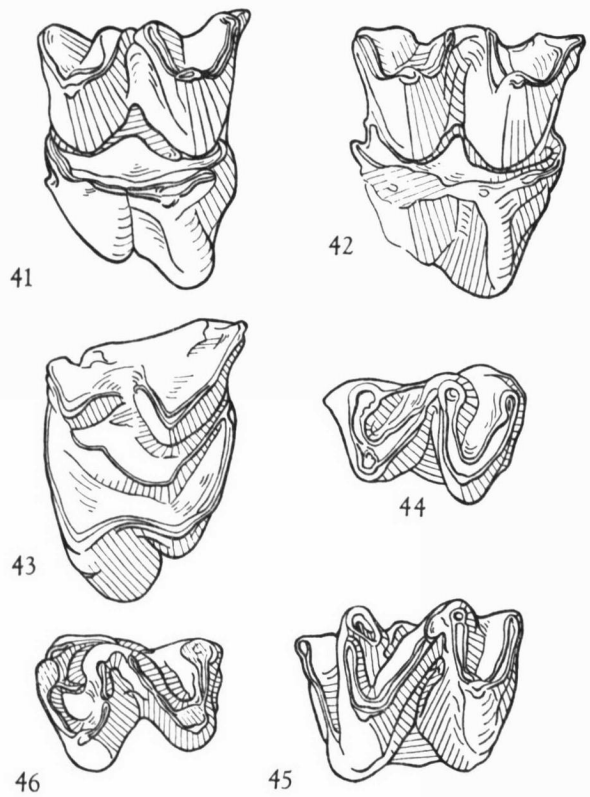
### PROSCALOPS sp. cf. P. SECUNDUS Matthew, 1909

Figures 41-46

Eleven isolated teeth from Quarry A agree in size and certain structural features, and are here regarded as

belonging to a single species closely related to *Proscalops secundus* of the lower Rosebud (early Miocene). These teeth are: KU10091 ($M^2$), KU10092 ($M^2$), KU10093 ($M^1$), KU10094 (two $M^{3}$'s), KU10095 ($M_1$), KU10096 ($M_2$), KU9358 ($M_2$), KU10097 ($M_3$), KU10098 ($M_3$), and KU10099 ($M_3$).

In size, *Proscalops* sp., cf. *P. secundus* is distinctly larger than *P. miocaenus* (MATTHEW, 1901, p. 375), but probably only slightly larger than *P. secundus* (MATTHEW, 1909, pl. 5). The only illustrations of *P. secundus* are photographs contained in MATTHEW's report on the Bridger Carnivora and Insectivora, and the only description is a brief comparison of *P. secundus* with *P. miocaenus* by GALBREATH (1953, p. 49). Study of the specimen itself has led me to think there may be no great difference between our specimens and the type except in larger size, and possibly, but by no means certainly, in relative size of $M^3$ (more enlarged in *P. secundus*); greater parastyle developed in $M^2$-$M^3$, and increased hypsodonty in the Martin Canyon species. It is difficult to make any significant comparisons with *P. secundus* because the specimens from Quarry A are fragmentary.




FIGURES 41-46. *Proscalops* sp. cf. *P. secundus*, all ×10. ——41, Right $M^2$, KU10092.——42, Right $M^2$, KU10091.——43, Left $M^1$, KU10093.——44, Right $M_3$, KU10099.——45, Right $M_2$, KU10096.——46, Left $M_3$, KU10098.

The upper molar pattern in *P. secundus* as figured by GREGORY (1910, p. 238) is inaccurate. I judge that GREGORY's outline drawing was made as an overlay on the photograph of MATTHEW showing a direct view of the occlusal surface. That drawing shows a pillar-like protocone and two large, deeply separated conules. Actual comparison with Quarry A specimens shows, however, little difference.

The teeth of *Proscalops* sp. cf. *P. secundus* have somewhat lengthened crowns, although shorter than in *Hesperoscalops* (HIBBARD, 1941) or *Scalopus* and may be described as mesodont. The hypsodonty is chiefly, but not entirely, of the unilateral type in which the internal part of the upper molars and the external part of the lowers is lengthened without a great amount of corresponding hypsodonty of the opposite sides.

$M^1$ is present only in a worn state in the collection, but several second molars are represented in fresh condition. This latter tooth is rather quadrate in outline except that the protocone bears a strong rib, which projects inwardly. This rib tapers upward so that with wear the occlusal outline becomes progressively more triangular. I can find no convincing record of the anterior conule, although a minute structure closely connate with the protocone could be the protoconule. A well-developed "hypocone" (metaconule?) is present, although not well separated from the protocone, which is nearly as large as the protocone. The hypocone is directly posterior to the unworn tip of the protocone, and hence external to the internal edge of the protocone rib. Viewed from their external sides, the protocone and hypocone are seen to be separated for a short distance from their tips by a notch. The mesostyle seems to be slightly divided on one $M^2$ available to me, but not in the other. The parastyle and metastyle are moderately pillar-like except that in KU10091 the parastyle is bifurcate. The rib of the protocone could, I suppose, be viewed as an independent structure at one time that has become fused with the protoconule (the other cuspule would then be the metaconule rather than the hypocone) with increasing hypsodonty. This would be in line with GREGORY's interpretation of the molar structures of *P. secundus*.

The third upper molar is represented by two teeth (KU10094), one with most of the external part missing. The protocone in this tooth also projects strongly internally with a consequent considerable potential change of outline as wear proceeds. The "hypocone," however, is here a much reduced structure, and although the metacone unites with the slightly bifurcate mesostyle, a metastyle is absent, and the metacone is hence a simple rather than a V-shaped ridge.

The lower molars all agree in the internal extension of the anterior crest of the hypoconid. That crest rises

well up the back side of the metaconid in $M_2$ and $M_3$ although in $M_1$ it terminates at its base, and nearly between the protoconid and metaconid. Anterior cingula are weak except in $M_2$. Posterior cingula are expanded internally into triangular processes on $M_1$ and $M_2$, and a slight cingulum is even present individually on $M_3$. The trigonids are compressed anteroposteriorly and have somewhat angulate protoconids. There is incomplete closure of the talonid valleys internally in all the molars. Relative height of cusps is much as is described for other moles from Quarry A except that there is a greater tendency for equality of height (most noticeable in greater relative talonid height) in connection with increased hypsodonty.

The first lower molar has a notably narrowed trigonid resulting in the tooth being wedge-shaped, and much broader across the talonid. The trigonid cusps, nevertheless, are relatively well separated.

$M_2$ is somewhat wider across the trigonid than across the talonid. A small cuspule helps block the internal entrance to the talonid valley. On the basis of available specimens, $M_2$ is slightly smaller than $M_1$.

$M_3$ is the smallest of the lower molars, but less reduced relatively than in $M_3$ of *P. miocaenus* (anteroposterior length about 27 percent of total molar length in contrast to 21 percent). The talonid is elongate and narrower than the trigonid.

*Measurements of* Proscalops *sp. cf.* P. secundus, *in Millimeters*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $M^3$, | ap | 3.0-3.2 | $M^3$, | ap | 2.3 | | |
| | tr | 3.4-3.7 | | tr | 2.2 | | |
| $M_1$, | ap | 3.4 | $M_2$, | ap | 3.0+-3.3 | $M_3$, ap | 2.4-2.6 |
| | tr | 2.5 | | tr | 2.3-2.5 | tr | 1.9-2.0 |

*Remarks. Proscalops* is seemingly known from middle Oligocene (Orellan) to late early Miocene (late Arikareean). So far as I know, all but one of the known specimens are either from northeast Colorado or South Dakota.[11] The single exception is a record cited by GALBREATH (1953, p. 49) from Wyoming. If all the referred specimens belong to *Proscalops,* the line of its species may have increased considerably in size and hypsodonty of the molars. But the presence of two species at Quarry A (see *Proscalops*? sp., beyond) suggests that two lines of descent are represented, possibly even generically distinct throughout much of their occurrence.

The relation of *Proscalops* to other moles has been variously interpreted by different authors. MATTHEW (1909, p. 539) thought that *Proscalops,* although primitive in several particulars, was specialized along lines paralleling the Chrysochloridae and different from those of moles. GREGORY and others suggested a relation to the water-moles, a suggestion that SCHREUDER (1940, p. 290) rejects.

Possibly a relationship to *Parascalops* should be considered, although GALBREATH compared the first known $M_2$ of *Proscalops* sp. cf. *P. secundus* to *Hesperoscalops,* an ancestor of *Scalopus* (1953, p. 93). *Proscalops secundus* has a dental formula of $\frac{3.1.4.3}{}$ with $I^1$ enlarged,[12] $I^{2-3}$, $\underline{C}$, and $Pm^{1-3}$ peglike, and $P^4$ much larger than the preceding premolars. Presence of a riblike protocone and of a "hypocone" suggest *Parascalops,* but enough hypsodonty had been acquired by Marsland (Quarry A) time to prevent, seemingly, an ancestral relationship to the short-crowned *Parascalops.* Seemingly, it would take considerable modification of the upper molars to lead into the type present in the higher crowned *Scalopus,* or other American moles. The needed transformation although not impossible suggests that *P. secundus* is aberrant.

### PROSCALOPS? sp.

Three isolated lower cheek-teeth, KU10100 ($M_1$), KU10101 ($M_2$), and KU10102 ($\overline{M}$, incomplete) represent a mole different from any of the preceding in size, and possibly in other characters as well. Possibly to be associated with these three teeth is an isolated $M^1$, KU10103.

The three lower teeth agree, except for their somewhat larger size, with specimens from the Orellan (middle Oligocene) of Colorado assigned by GALBREATH (1953, p. 49) to *Proscalops* sp. (small form). The only tooth in the two lots that can be compared satisfactorily is $M_2$. Other than in size, the Quarry A specimen, KU-10101, probably has relatively higher crowns and possibly a greater triangular expansion of the posterior cingulum. Possibly, also, the hypoconid pillar on $M_1$ is more angulate in KU10100 from Quarry A than in an incomplete $M_1$ of KU8143 referred by GALBREATH to *Proscalops* sp. (small form). Otherwise, I can see no difference in the two lots of material. In size, the Quarry A species nearly reaches that of *Proscalops miocaenus* of the late Oligocene, but seemingly is slightly smaller.

The $M^1$, KU10103, is of the right size to be associated with the lower molars, but possibly represents a shorter-crowned species (such as a large species of

[11] The specimen from the lower Rosebud, assigned by GREEN (1956, p. 152) to an unnamed species of *Domninoides,* possibly represents the lower jaw of *Proscalops secundus.* It apparently is much less well preserved ($M_1$-$M_3$ only?) than the type specimen of *Domninoides riparius* and some of the characters which would separate *Domninoides* from *Proscalops* need not apply.

[12] SCHREUDER *(loc. cit)* suggested that the enlargement of the incisor stated to be present, and which has been referred to by authors, is a fiction based on an attempted restoration by MATTHEW of *P. miocaenus.* SCHREUDER was in error, for she had assumed that there is only one specimen of *Proscalops,* the type specimen of *P. miocaenus.* The Rosebud specimen shows a large alveolus for $I^1$, and otherwise permits the recognition of the character of the anterior teeth, and of the dental formula.

*Scalopoides*). The inner border of the tooth seems much less sharply triangular than that of $M^1$ in the type of *Proscalops miocaenus,* and the paracone cusps may differ although in neither KU10103 which is much worn or in the figure of *P. miocaenus* can the exact shape be certainly determined. In the type description of *P. miocaenus,* MATTHEW (1901, p. 375) writes of a "very rudimentary hypocone" in $M^1$. His figure shows none at all. A small hypocone that I would describe as "very small" in comparison with that of *Proscalops secundus* is present in KU10103.

*Proscalops?* species differs from *Proscalops* sp. *cf. P. secundus* not only in distinctly lesser size, but also in (a) more acute protoconid-hypoconid pillars, (b) a more attenuated shape to the molars that tend to be pinched in at the talonid-trigonid junction, (c) possibly greater crown height, and (d) much less development of the hypocone if the upper molars are properly assigned.

Comparing only *Proscalops?* species and *Proscalops* sp. *cf. P. secundus,* I have received the impression that these pertain to different genera. I am referring KU10100-KU10103 tentatively to *Proscalops* on the basis of agreement with *Proscalops* sp., Galbreath, 1953.

*Measurements of* Proscalops? *sp. in Millimeters*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $M^1$, | ap | 2.5+ | $M_1$, | ap | 2.4 | $M_2$, ap | 2.5 |
| | tr | 3.0+ | | tr | 1.9 | tr | 2.0 |

**SORICOID? sp. indet.**

An isolated first upper molar, KU10104, seemingly represents some kind of soricoid. It does not appear to be quite like $M^1$ of any kind of insectivore named from Quarry A. The $M^1$ lacks the characteristic posterior cingulum of *Heterosorex*. The inner half of the $M^1$ resembles those of the upper molars referred to *Scalopoides isodens,* but otherwise lacks the characters of *Scalopoides*. KU10104 possibly is chiropterid, but heavy wear across the external faces of the paracone and metacone prevents extensive comparisons, if indeed it is possible in any case to identify an isolated tooth so primitive and generalized as this one seems to be. Measurements of KU10104 ($M^1$) are ap, 2.0 mm.; tr, 1.9 mm.

## Order LAGOMORPHA

Lagomorph specimens are rather common at Quarry A, but with few exceptions they consist of isolated teeth and fragmentary limb bones only.

Unlike most Tertiary occurrences of lagomorphs in North America, not only are ochotonids as well as leporids represented in the collection, but additionally, the former are distinctly in the majority.

## Family LEPORIDAE

**HYPOLAGUS? sp.**

Several isolated teeth, KU10106, represent a leporid in the fauna, possibly of the genus *Hypolagus* (DAWSON, 1958, p. 44-45). If this genus is in fact present, it is one of the earliest occurrences on record.

## Family OCHOTONIDAE

**OREOLAGUS nr. O. NEBRASCENSIS Galbreath, 1953**

As stressed by GALBREATH (1953), the lower cheek-teeth of the Quarry A species are longer than wide, and stage of wear does not seem to alter this proportion. Occasionally, a tooth is found with the reverse proportions, but sufficient specimens are now available to establish the long tooth as characteristic. In the type of *O. nebrascensis,* the transverse diameter exceeds the anteroposterior one. Until sufficient material of *O. nebrascensis* from the type locality becomes available to decide what the usual proportions are, it is best to maintain GALBREATH's tentative assignment.

Additional superior cheek-teeth (KU10108-KU10109, KU10115, KU10117) now available show that isolated external crescents (in some specimens more than one), and relatively short internal hypostriae are characteristic of $P^4$-$M^2$. $M^3$ is absent. The structure of these upper molars differs from those designated as *Oreolagus?* n. sp. by WALLACE (1946, p. 126) from the Beatty Buttes local fauna. The latter have deep, straight hypostriae like those of *Ochotona*. Which of the two patterns is present in *Oreolagus (s.s.)* cannot be established, but the striking similarity of the Beatty Buttes maxillary to the Recent *Ochotona* suggests that the Quarry A pattern is the one possessed by *Oreolagus*.

The mandible of *O.* nr. *O. nebrascensis* (KU9815, KU10112-KU10114) has several points in which it resembles the leporids more than it does *Ochotona* (MACINNES, 1953). Some of these are: (1) the coronoid process is derived from the outer of the two flanges of the anterior border of the ascending ramus, rather than from middle of the relatively flat anterior face; (2) the main aperture of the dental foramen is well below the level of the tooth row; (3) the anterior mental foramen is in front of $P_3$; and (4) the articular surface of the jaw occupies nearly all of the upper surface of the condyle. Nevertheless, *Oreolagus* from Quarry A is clearly ochotonid. The upper incisor alone is quite characteristic, but in addition, there are details in the other teeth, jaws, and some foot bones which indicate this. Most other ochotonids, or supposed ochotonids, from the earlier part of the Miocene exhibit this same mingling of "characters" of the two existing families of lagomorphs. The failure to record ochotonids in the late Eocene, and the divergence of opinion as to whether certain Oligocene lagomorphs—*Desmatolagus* and *Amphilagus*—are one or the other,

all suggest to me that the two groups diverged from a common ancestry during the Oligocene.

It is well known that the lagomorph record of Europe is essentially one of ochotonids. Indeed, it is not until late Miocene or Pliocene times that clearly leporid species appear. Asia has much the same type of record as Europe except that supposed leporids are recorded from the late Eocene. Quite the contrary aspect is seen in North America where undoubted leporids are common Oligocene-Miocene fossils, and ochotonids are always rare, and possibly absent in the Oligocene. Thus, the Old World was clearly the area of development of the Ochotonidae, as America presumably was of the Leporidae. If the consensus of opinion is correct, in excluding *Desmatolagus* and *Amphilagus* from the latter family, then leporids, exclusive of the late Eocene species, did not occupy Eurasia until the close of the Miocene.

Contrary to an earlier statement of mine (WILSON, 1949b, p. 131) where I accepted the opinion of BURKE (1936, 1941), I feel that assignment of *Desmatolagus* and *Amphilagus,* as well as other Old-World genera contemporaneous with them, to the Ochotonidae is not prevented by the anatomical facts now known, and is, moreover, in harmony with the general geographic picture. In any case, it seems inconsistent to refer *Titanomys* to the Ochotonidae (SIMPSON, 1945, p. 75-76) and the closely related *Amphilagus* to another division of the lagomorphs. Either there are no known European ochotonids of Oligocene and Aquitanian age, or no known leporids. A specimen of *Titanomys visenoviensis,* according to FORSYTHE MAJOR (1899, p. 486), shows a palate already evidently ochotonid. Limb bones of this species suggest much the same thing. Nevertheless, *T. fontannesi* (a species sometimes referred to *Titanomys* and sometimes to *Amphilagus*) does have some notably non-ochotonid features—for example, in specimens available to me, the short lower incisor that reaches to the anterior edge of the alveolus of $P_3$ only. This is a characteristic of advanced leporids.

Ochotonids, on the other hand, were present in North America throughout the middle and later Tertiary, but apparently always enjoyed only indifferent success in the environments represented in the fossil record.

The abundance of ochotonid remains at Quarry A seems to be fundamentally the result of environmental factors. These same factors have produced a microfauna that bears a decided resemblance to that of Europe. In view of the generic identity with those of Europe of several of the insectivores *(Plesiosorex, Heterosorex)* and rodents *(Pseudotheridomys, Plesiosminthus),* it would be supposed that *Oreolagus,* too, had some close European relatives. Such, however, does not seem to be the case. Three of the Aquitanian and Miocene European genera *(Piezodus, Prolagus, Lagopsis)* have much more complicated third lower premolars (VIRET, 1929). *Titanomys,* also, has a somewhat more complicated $P_3$, and in addition (and also like *Piezodus* in this regard), the upper cheek-teeth are distinctly shorter crowned, in fact root-bearing. Of the known European genera, only *Amphilagus* has a $P_3$ close to that of *Oreolagus.* MCGREW (1941) commented on the resemblance of *Amphilagus, Desmatolagus,* and *Oreolagus,* and thought that *Desmatolagus* might be ancestral to the last named. BURKE (1941, p. 13), although of the opinion that *Amphilagus* and *Desmatolagus* were not ochotonid, also suggested a possible special relationship between these two genera. Finally, GALBREATH (1953, p. 94) found nothing in the additional upper cheek-teeth of *Oreolagus* available to him that would prevent *Desmatolagus* from being ancestral to the former. He did, nevertheless, recognize several rather considerable differences between *Amphilagus* and *Oreolagus. Amphilagus* is reported at both older (upper Stampian) and younger (La Grive St. Alban) stratigraphic levels than *Oreolagus* nr. *O. nebrascensis.* Still $M_3$ is always present; the lower cheek-teeth (exclusive of $M_3$?) have a weak third lobe in early stages of wear; and the upper molars are short crowned with distinct roots. *Titanomys* has lost $M_3$, but otherwise the same lack of progress toward hypsodonty is evident. They both agree with *Oreolagus* nr. *O. nebrascensis* in the retention of the crescents of the upper molars, although the crescents are much more clearly retained in the European genera. *Desmatolagus* seems to be a more logical ancestor to *Oreolagus* than anything in Europe, whatever the actual ancestry is. This has been recognized by previous authors (MCGREW, GALBREATH). The main points here, however, are to emphasize that the European record seemingly does not contain the genus *Oreolagus* under a different name, and that the ultimate source of *Oreolagus* is to be sought in North America or eastern Asia rather than in Europe. Nevertheless, *Desmatolagus, Amphilagus,* and *Oreolagus* have a number of points of similarity, and may well have, as suggested by others, a special relationship to each other.

It is perhaps of interest to note that all European Oligocene and Aquitanian lagomorphs *(Amphilagus, Piezodus, Titanomys)* are relatively short crowned (shorter crowned than *Oreolagus*), and retain upper molar crescents. *Oreolagus* seems evidently more progressive than these. In the Burdigalian, *Lagopsis, Prolagus,* and *Titanomys* (ROMAN & VIRET, 1934) have been reported. Here then are species at least as advanced as *Oreolagus* and actually more advanced in the stage of reduction of the crescents and the increased depth of the internal reentrant angles. *Kenyalagomys* (MACINNES, 1953) of the early Miocene of Africa also has high-crowned teeth without external crescents, and with deep internal reentrant angles in the upper molars. Somewhat more progressive species than those from the Burdigalian are known from the Vindobonian of Europe

where *Amphilagus* or *Titanomys, Prolagus,* and *Lagopsis* are found. Thus, in regard to stage of evolution, the Quarry A ochotonid seems to be advanced over those of the Aquitanian of Europe, but seemingly less advanced than some in the Burdigalian.

## Order RODENTIA

As is true of the Insectivora, the Order Rodentia is represented at Quarry A by numerous, but fragmentary specimens. Also like the insectivores, the rodents show special affinities with those of European faunas. The resemblance is perhaps less striking for two common groups of rodents from Quarry A, the Mylagaulidae and the Heteromyidae, are restricted to North America, and these constitute 40 percent of the total rodent fauna. Nevertheless, two extinct European genera, *Pseudotheridomys* and *Plesiosminthus,* are identified, and the beavers and squirrels appear to be closely related on the two continents. One additional myomorph in the fauna is not far removed from European relatives. With some taxonomic juggling it is possible to maintain that 45 percent of the genera of Quarry A are to be found in Europe. Moreover, if representatives of the strictly North American families are excluded this figure is increased to 70 percent.

## Suborder SCIUROMORPHA

Almost all workers of the past few years have stressed the artificial nature of the old suborder Sciuromorpha. I have been reluctant, however, to abandon the familiar term, and to recognize formally these trends of thought. It is much easier to destroy the old than to replace it with anything that two or more workers will support. There comes a time, however, when it is useless to continue, any longer, an obviously wrong taxonomic arrangement. My present arrangement conforms to the classification proposed by A. E. WOOD (1955).

Two families of rodents from Quarry A I believe to be probably validly associated under the name Sciuromorpha. These are the Mylagaulidae and the Sciuridae. The other "sciuromorph" families represented at our locality, I am placing elsewhere.

### Family MYLAGAULIDAE

A single genus and species, *Mesogaulus paniensis,* is represented. Although probably the most primitive species of the genus, it is still considerably beyond *Promylagaulus* of the earlier Miocene in stage of evolution, particularly in size and in height of crown of tooth. *M. paniensis* is one of the relatively few Quarry A species that suggests closer relationships of the Marslandian to the Sheepcreekian than to the Harrisonian.

**MESOGAULUS PANIENSIS (Matthew, 1902)**
Figures 47-59

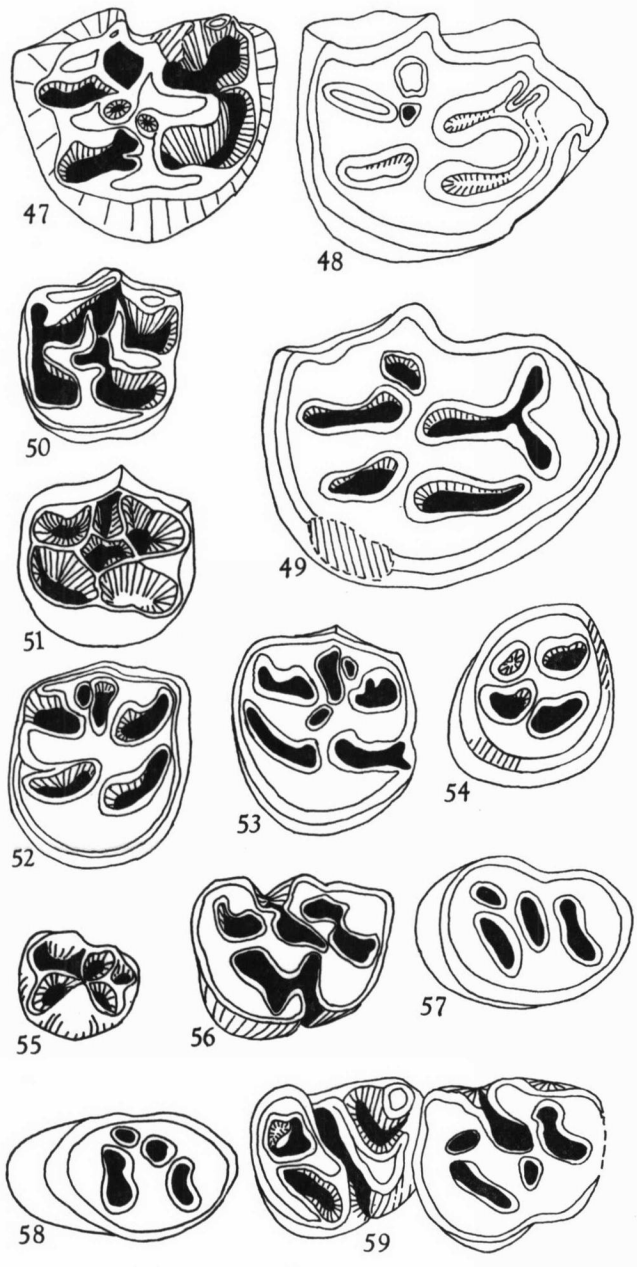
*Mesogaulus praecursor* COOK & GREGORY, 1941.
*Mesogaulus paniensis* GALBREATH, 1953 (p. 95).

*Mesogaulus paniensis,* I judge, is the oldest as well as the most primitive known species of Mesogaulus. Indeed, only two species of mylagaulids older than *M. paniensis* have been named, *Promylagaulus riggsi* (lower Rosebud) and *Mylagaulodon angulatus* (John Day?). Each of these is known by only two reported specimens. Thus, the acquisition of a number of specimens of *M. paniensis,* fragmentary although they are, is a welcome addition. All teeth, save $Dp^3$ and $Dp_4$, are represented in an unworn or little worn state. Because figures of mylagaulids are on the whole satisfactory without accompanying descriptions, the specimens from Quarry A (Figs. 47-59) are not here described in detail. Primitive features shown by the relatively unworn specimens are discussed.

The only cranial fragment available to me (KU160) has, on the frontals, small postorbital processes that seemingly project somewhat posteriorly. The supraorbital ridges of the skull are obscure. The muzzle seems relatively wide in comparison with some later forms. The rear of the skull, as indicated by what little of the braincase is preserved, seemingly was not widened so much as in later mylagaulids.

$P^3$ is present as a small, simple cone in this species. It persists in the jaw at least for a moderate length of time.

$P^4$ is known by several specimens (KU10120-KU-10124, KU9292) that show not only variation with age and wear, but apparently some individual variation not related to wear alone. The tooth has an outline closely resembling that figured for *Mylagaulodon* (MCGREW, 1941), that of *Mesogaulus praecursor* (COOK & GREGORY, 1941), and even that of *Liodontia,* but is unlike late Miocene specimens (*M. novellus* is a partial exception: BLACK & WOOD, 1956) in being relatively wide posteriorly and in having angulate, or irregular, borders instead of the rather smoothly oval outlines of the later species. These differences in shape are associated with the posterior position of the protocone, and varying development of parastyle, paracone rib, mesostyle, and metastyle processes. The mesostyle, especially, is usually quite rib-like in early stages of wear. A channel running the height of the tooth is well-developed in front of the mesostyle. Lesser channels are present anterior to the metastyle, alongside the parastyle, and elsewhere. The pattern of $P^4$ is like that of the following molars in the jaw except for the development of a parastyle. Protoconule and metaconule are both well developed. Crests from these cuspules join internally and as a result there




FIGURES 47-59. *Mesogaulus paniensis.*——47, Right $P^4$, KU10121.——48, Right $P^4$, KU10122.——49, Right $P^4$, KU10123.——50, Left $M^1$, KU10128.——51, Left $M^2$, KU10135.——52. Right $M^2$, KU10139.——53, Left $M^2$, KU10132.——54, Right $M^2$, KU10136.——55, Left $M^3$, KU10129.——56, Right $M_1$, KU10137.——57, Right $M_2$, KU10142.——58, Right $M_3$, KU10146.——59, Right $M_1$-$M_2$, KU10138. [All ×6 except Figs. 56-58, ×6.5.]

is only a single one leading to the protocone. A short crest from the protoconule extends to the paracone, and a similar one unites metaconule with metacone. Other spurs from the protoconule and metaconule tend to join in a knot in the center of the tooth giving rise to several small, short-lived, lakelets as the tooth is worn. The protoconule is separate from the anterior cingulum in the unworn state, but the posterior wall of the metaconule is continuous with the posterior wall of the tooth even in the fresh state. In most stages of wear five fossettes are present, a large y-shaped anterior one, a small parafossette, and moderately developed metafossette, protofossette, and hypofossette (as these names are used by COOK & GREGORY, 1941, and somewhat differently from those of BLACK & WOOD, 1956).

$Dp^4$ (KU10119) has the same pattern as $P^4$ except that the parastyle is more developed, and the metaconule is slightly detached from the posterior cingulum. $Dp^4$ is, of course, considerably smaller and shorter crowned. The pattern closely resembles that of $Dp^4$ of *Liodontia,* perhaps more so than it does $P^4$ (permanent) of *Meniscomys.*

The first upper molar is best represented by KU 10128. This tooth is short crowned in comparison with $P^4$, $M^2$, and $M^3$, but is longer crowned than $Dp^4$. KU-10128, as in the other upper cheek-teeth, has a more strongly hypsodont inner than outer tooth wall. The most notable feature of $M^1$, as viewed laterally, is its wedge-shaped outline. The only prominent style is the mesostyle. The pattern of the crown, less the parastyle, is nearly the same as that of $P^4$ except for the more quadrate shape of the tooth. $M^1$ is like $M^2$. The resemblance to $M^1$ of *Meniscomys* is also marked (MCGREW, 1941a, fig. 7).

The second upper molar (KU10132-KU10135), except for its greater length of crown, has essentially the same structure as $M^1$. The occlusal pattern is nearly identical to that of $M^1$. In rather worn teeth, the pattern is transformed into one of four lakes. The pattern of $M^1$ resembles that of *M. novellus* (BLACK & WOOD, 1956, fig. E) except that the mesostyle extends nearly to the base of the tooth.

The third upper molar is reduced relative to $M^2$, but is nevertheless hypsodont. The same pattern prevails, but the posterior half is somewhat aborted. For this reason, the mesostyle has been reduced considerably. The metacone is no longer a distinct cusp, but simply a point on the posterointernal border of the tooth. Five miniature basins can still be seen in the unworn tooth of one specimen, KU10129, but in another, KU10130, the posteroexternal one is absent. The pattern is, nevertheless, less reduced than in *M. novellus* which seems to have, characteristically, only three lobes. $M^3$ is anomalous in being as reduced in size, perhaps slightly more reduced, in *M. paniensis* as in *M. novellus.*

Not enough of the lower jaw (KU160) is preserved to warrant any statement except that so far as preserved, it is comparable to the type of *Mesogaulus paniensis.*

The fourth lower premolar is known from seven specimens (KU9197, KU9293, KU9364, KU9370, KU10125-KU10127), most of which were figured by GALBREATH (1953, p. 95). A really early stage of wear is not available. It is obvious, however, that a strong resemblance to $P_4$ of *Meniscomys* is present, including the presence of some sort of mesostylid (or metastylid). A possible fragment of $Dp_4$ is too incomplete for description.

The first lower molar is represented by several specimens; the pattern is best seen in KU10137. As in $M^1$, this tooth is much shorter-crowned than other cheek-teeth, and is notably wedge-shaped as viewed laterally. It resembles $M_1$-$M_2$ of *Meniscomys* in the presence of a large mesostylid (metastylid) cusp, and in the relatively great width of the heel, which imparts a lobate appearance to the tooth. It is basically similar in pattern to *M. novellus,* but seemingly more complex. A specimen having a more clearcut pattern is available for $M_2$, and the details of the pattern (other than what can be observed in figure 57) will be described only for the latter tooth. In comparison with $M_2$, $M_1$ differs in addition to the presence of a metastylid and more lobate outlines, in the thinness of enamel in places, and in a somewhat more complicated series of connections of parts in the trigonid area, partly the result of the prominence of the metastylid.

A jaw fragment, KU10138, has a little worn second molar in association with $M_1$. No other lower molar so clearly shows the basic pattern as does this one. The metaconid is a relatively high, simple cone, and the protoconid seems to differ only in being slightly more crescentic, and slightly less elevated. The short anterior arm of the protoconid reaches to the flank of the metaconid. In the present stage of wear, the point of juncture is slightly notched. The posterior arm of the protoconid is long and directed obliquely backward, reaching to the inner margin of the tooth. The metastylid (mesostylid) is absent or more likely indistinguishably fused with the arm. Only a slight notch separates the posterior arm from the posterior surface of the metaconid. Thus a large basin (anterofossettid of COOK & GREGORY is the closest term, but this lake in $P_4$ and in the molars is probably only partly homologous) is isolated in the trigonid area of the tooth; this basin is usually subdivided in moderately worn $M_1$. In length of posterior arm, $M_2$ is like the molars of the cricetid, *Eumys.* Behind the trigonid is the large and somewhat centrally placed (more so in $M_1$) mesoconid. The mesoconid is obliquely oriented. Its anteroexternal edge touches and is partly fused to the trigonid. More posteriorly, two crests diverge from the mesoconid: one is the hypolophid, which joins the entoconid; the other is what is present of the ectolophid and reaches to the hypoconulid area of the posterolophid. Thus a second basin is isolated (metafossettid of COOK & GREGORY) and it is partly divided by a spur of enamel in KU10138. A third basin (mesofossettid of COOK & GREGORY) on the inside of the tooth is shut off by a ridge extending from entoconid to inner end of the posterior protoconid arm to metaconid. In the heel area, the entoconid appears to be continuous with the posterolophid although distinctly a cusp in early stages of tooth wear. The hypoconid is greatly attenuated, and this configuration together with the development of an ectostylid results in closing off a posteroexternal basin (hypofossettid of COOK & GREGORY), the second of the two usually recognized in the "talonid" region of the tooth. The shape of the hypoconid and the tendency to shut off some sort of a basin is seen in varying degrees in *Eohaplomys, Sciurodon,* and *Plesispermophilus* (STEHLIN & SCHAUB, 1951, figs. 484, 489, 469). The anteroexternal side of the mesoconid borders a small, less well-developed and rather narrow, depression that would exist as a small fossettid (protofossettid of COOK & GREGORY) in certain stages of wear. Probably six, possibly seven, fossettes could be present as wear proceeds. In most stages four would be present (anterofossettid, mesofossettid, metafossettid, and hypofossettid), and even in advanced wear all but the metafossettid of these four linger on. It may be observed that a comparison of premolars and molars suggests that the cusp termed the metaconid by COOK & GREGORY is the metastylid (or mesostylid), and that termed "paraconid" is the metaconid. So far as homologies are concerned, it would be better perhaps to rename the fossettids as follows:

*Suggested Revised Nomenclature of Mylagaulid Fossettids*

| COOK & GREGORY | WILSON |
|---|---|
| anterofossettid (a) | anterofossettid (b) |
| metafossettid | metafossettid |
| mesofossettid | entofossettid |
| hypofossettid | mesofossettid |
| protofossettid | hypofossettid |
| | protofossettid |

(a) Small lake only in $P_4$ (or part of ?anterofossettid)
(b) Not much represented in molars.

Some differences between *M. paniensis* and *M. novellus* are to be seen, as for example in the less continuous ectolophid of the former, but how significant those differences are I do not know. The patterns are fundamentally the same.

The pattern of $M_3$ can be seen best in an unworn tooth, KU10139. As in $M^3$, the posterior half of $M_3$ is much reduced. A distinct metastylid is present, which reenforces the view that in $M_2$ this cusp is present but indistinguishably fused with the protoconid area. The transversely elongate anterofossettid (metafossettid of

right column above) is the largest fossettid of the tooth, and seemingly can become divided into two parts in certain intermediate stages of wear. In early stages of wear, mesofossettids and metafossettids (entofossettids of above) are united as an anteroposteriorly extended basin, but they later divide. So far as can be ascertained, only a single fossettid for the combined hypo- and protofossettid is present. I presume that it is principally the hypofossettid. Comparison with *M. novellus* is difficult, but as in the other molars, $M_3$ of *M. paniensis* seems to have a more complex pattern. $M_3$ in *M. paniensis* is relatively less reduced in relation to $M_2$ than in *M. novellus*.

Rather distinct roots, and a fairly heavy coating of cement (at least over the roots and lower part of crown) become evident in advanced wear. $M_2$ may in old age be difficult to distinguish from $M_1$ in a less advanced stage of wear. Lack of specimens of the aplodontid *Meniscomys* in which the teeth are only slightly worn prevents much meaningful comparison of the molars of *Mesogaulus* with those of *Meniscomys*.

*Measurements of* Mesogaulus paniensis (KU160), *in Millimeters*

| | | |
|---|---|---|
| Breadth of rostrum | 16.0 | |
| Diastemal length (I-$P^3$) | 12.5 | |
| Width of skull at postorbital constriction | 12.9 | |
| Length of postorbital process | 4.0 | |
| $\underline{I}$, ap | 3.8 | |
| tr | 3.5 | |
| $P^4$, ap (occlusal) | 7.0 | |
| tr (occlusal) | 6.2 | (approx.) |
| $\underline{I}$, ap | 4.3 | |
| tr | 3.2 | |
| $P_4$, ap (occlusal) | 6.6 | |
| tr (occlusal) | 5.0 | |

*Upper Cheek-teeth from Quarry A*

| | $Dp^4$ | $P^4$ | $M^1$ | $M^2$ | $M^3$ |
|---|---|---|---|---|---|
| Internal crown height(a) | 2.6 | 7.3-10.5 | 4.0 | 6.9-8.4 | 4.0-5.0 |
| Max. ap diam. | 4.3 | 7.2-8.8 | 3.6 | 3.8-4.0 | 2.5 |
| Max. tr diam. | 4.5 | 5.6-6.0 | 4.2 | 4.3-4.6 | 2.4-2.5 |

(a) From enamel edge between roots to occlusal surface.

*Lower Cheek-teeth from Quarry A*

| | $P_4$ | $M_1$ | $M_2$ | $M_3$ |
|---|---|---|---|---|
| External crown height(a) | (5?)7.3-9.9 | 3.6 | 3.9-7.5 | 5.2 |
| Max. ap diam. | 7.0-8.9 | 4.0-4.1 | 3.9-4.0 | 3.5-3.6 |
| Max. tr diam. | 4.0-4.6 | 3.4-3.5 | 3.2-3.25 | 2.7-2.9 |

(a) From enamel edge to occlusal surface.

A characteristic of *Promylagaulus* calls for comment. In the lower molars only a single talonid lake is present. McGREW (1941, p. 21-22) comments on the presence of two talonid lakes in *Meniscomys* and two in most later mylagaulids. He says "due to the absence [in *Promylagaulus*] of the ridge running forward from the hypoconulid, the two lakes found in *Meniscomys* are united. However, this last character cannot be regarded as significant because the ridge between the talonid lobes is present in some specimens of *Mylagaulus* and absent in others belonging to the same species." This is, I think, misleading as a description, and the difference is perhaps not so easily dismissed as McGREW supposed. Unworn molars of *M. paniensis* show, as previously indicated, that the more internal of the two fossettids in question is an "orthodox" talonid pit enclosed by the posterolophid, entoconid, and hypolophid. The more external one, however, is formed from the posterior half of the external valley between protoconid and hypoconid. It is in fact enclosed by the hypoconid, ectolophid-mesoconid, and ectostylid structures. The ridge spoken of by McGREW is then the posterior end of the ectolophid that must have been present also in *Promylagaulus*. Whether the difference in the number of lakes is the result of a difference in structure (lack of attenuation of the hypoconid), or a result of wear obliterating this second lake cannot be decided at present. If the former, it might tend to place *Promylagaulus* off the main line of descent leading to the typical mylagaulids.

Within the genus *Mesogaulus*, it has been assumed by COOK & GREGORY and by Galbreath that *M. praecursor* was the oldest and most primitive species. This was, I think, a view based on inadequate material of both species, together with an erroneous idea of the age relations of *M. paniensis*. If the Quarry A species is *M. paniensis*, which it almost surely is, then not only is the latter as primitive as the former and of equivalent age, but the two are probable synonyms. GALBREATH (1953, p. 96) stated that the two were closely related, but attempted to distinguish between them by supposing that *M. paniensis* was: (1) of larger size, (2) more hypsodont, and (3) of simpler occlusal pattern in having an earlier, or total, loss of some of the smaller lakes. But the additional specimens from Quarry A include some that are larger and some that are smaller than those of *M. praecursor*. Comparison of teeth having the same stage of wear as judged by the occlusal pattern

*Tooth Measurements of* Mesogaulus praecursor *(HC137) and* M. paniensis *(KU10121, KU10124, KU10126) from Quarry A*

| | HC137 rt. $P^4$ | HC137 left $P^4$ | HC137 $P_4$ | KU10121 $P^4$(a) | KU10124 $P^4$(b) | KU10125 $P_4$(c) | KU10126 $P_4$(c) |
|---|---|---|---|---|---|---|---|
| Crown height | 7.4 | 10.5 | 7 | 10.9 | 7.3 | 7.3 | ?5 |
| Max. ap diam. | 7.8 | 7.7 | 7.9 | 7.9 | ..... | ?8.3 | 8.0 |
| Max. tr diam. | 5.8 | 6.0 | 4.2 | 5.8 | 5.6 | ..... | 4.0 |

(a) Less worn than left $P^4$ HC137.
(b) Same stage of wear as HC137 rt. $P^4$.
(c) Same stage of wear as $P_4$ HC137.

shows no decisive difference in hypsodonty. The foregoing tabular material demonstrates these points.

Lastly, as for differences in pattern mentioned by GALBREATH, KU10123 is almost identical to HC137 left $P^4$ except for one small lakelet. In another specimen, KU10121, this structure and an additional one is present. Likewise, KU10126 is identical with HC137 $P_4$ except for a tiny lakelet that is present in other specimens from Quarry A. BLACK & WOOD (1956, p. 684) state that *M. novellus* is smaller, and hence presumably more primitive than any other species of this genus. They state elsewhere that the premolars are much lower crowned than in other species, and give measurements of three of them. These measurements suggest a crown approximately 25 percent shorter than in *M. paniensis*. Nevertheless, almost certainly, *M. praecursor* and *M. paniensis* are older geologically than is *M. novellus*. Those authors state that in the anterior position of the protocone and in the smaller size of the mesostyle *M. novellus* suggests a more advanced species than *M. praecursor*. Not only do shortness of crown and weak mesostyle seem to be opposed characters, but also the Quarry A molars showing little or no wear seem more reminiscent of ancestral patterns than those figured by BLACK & WOOD, and hence suggest less reduction than there is in *M. novellus*. It should also be noted that COOK & GREGORY (1941, p. 552) refer to undescribed specimens in the American Museum collections that "may belong to *M. novellus*": these are described by them as the only known permanent mylagaulid teeth smaller than those of *M. praecursor* in length and breadth (except *M. angulatus*), and differing also in their higher crowns.

Regardless of whether or not the crowns in *M. paniensis* are really higher (or relatively higher since they are larger in other dimensions) than in *M. novellus*, the totality of characters suggests that it is a less advanced species than *M. novellus*.

The type of *Mesogaulus paniensis* is from the Pawnee Butte area rather than Martin Canyon. Late Arikareean deposits are probably present however in the former area, and the type is from beds at the base of the Miocene section. Insofar as comparisons are possible, the type is identical with our material.

COOK & GREGORY (1941, p. 551) have commented on a certain similarity of tooth-pattern shown by *M. praecursor* and the geologically younger *Ceratogaulus rhinoceros*. They did not think the pattern was indicative of any special affinity between the two. That there is some special relationship, however, is suggested by the fact that the type specimens of *C. rhinoceros* and *M. paniensis* are from the same geographic area.

European "aplodontids" are not close in pattern to *Mesogaulus*. That of *Sciurodon* is, however, similar to the American *Allomys*, and may be regarded tentatively as an aplodontid. *Sciurodon* differs from *Mesogaulus paniensis*, *Meniscomys hippodus*, and possibly, although not clearly, from *Allomys* and *Eohaplomys* in that, in the European genus, the protoconule and metaconule have separate connections with the protocone in the upper cheek-teeth. In *Meniscomys* and *Mesogaulus* a single ridge extends from the protocone and then forks, sending a branch to the metaconule and one to the protoconule. Lacking specimens of *Allomys* and *Eohaplomys*, I cannot be sure what the situation is like in those genera, but judge that they lack these ridges or have ridges resembling those of *Meniscomys* more than those of *Sciurodon*. *Ameniscoides* DEHM (1950) is also remote from *Mesogaulus* and seems to be farther removed from North American aplodontids than is *Sciurodon*. *Pipestoneomys* (DONOHUE, 1956, p. 267) and *Ameniscoides* are regarded by Donohue as "superficially rather more alike than either is to the other aplodontids." This author concludes, however, that no direct relationship seems likely.

*Mesogaulus* is certainly closer to *Meniscomys* than to other genera of known American aplodontids. Nothing can be added to previous statements of authors, especially MCGREW (1941).

*Promylagaulus* and *Mylagaulodon* are the two earliest genera of mylagaulids. *Promylagaulus* from the lower Rosebud is a much smaller species than *M. paniensis*, and distinctly more primitive in various ways. [SCHULTZ & STOUT (in manuscript) record *Promylagaulus* in the Marsland. If this record is correct, then certainly the later species of this genus are aberrant.] *Mylagaulodon* is apparently also more primitive than *M. paniensis*. Nevertheless, the $P^4$, from the upper Rosebud, assigned by MCGREW (1941a, p. 9) to *Mylagaulodon cf. angulatus*, is only slightly smaller than *M. paniensis*, and the pattern of fossettes is essentially the same. The general outline of the tooth is alike in the two species. Nevertheless, *M. cf. angulatus* is seemingly less advanced than *M. paniensis*, in having mesostyles that are more persistently riblike (as figured); if *angulatus* is the less advanced, the upper Rosebud may not be so high stratigraphically as the Martin Canyon local fauna.

It has been proposed by DORR (1952) that the dental formula in *Mesogaulus*, and presumably all later mylagaulids, is $\frac{1.0.1.2}{}$. $M_3$ is regarded by him as absent, the tooth usually identified as $M_1$ as $Dp_4$, and that usually identified as $Dp_4$ as $Dp_3$. These conclusions were based on specimens representing several species of *Mesogaulus*. DORR's interpretation has been supported by DOWNS (1956, p. 215), and attacked by MCKENNA (1955, p. 109), and by BLACK & WOOD (1956, p. 677-678). I am strongly of the opinion that DORR is wrong.

Any brief summary of DORR's arguments obviously does him an injustice, but his case seems to rest essentially on the structure of the tooth identified as $Dp_4$ by him and as $M_1$ by MATTHEW and others. This tooth is short-crowned with two long roots and is unlike the hypsodont teeth before and behind it. Hence, it must be, accord-

ing to him, a different kind of tooth, a deciduous tooth. Almost all other points that DORR makes are secondary to this. Yet I think it difficult to imagine a tooth occupying the space available that would still retain a full suite of molar features. Teeth of *Mesogaulus paniensis* from Quarry A are either geologically older than DORR's or ontogenetically younger, or both, and retain more of the "molar structure." These teeth ($Dp_4$ or $M_1$) are wedge-shaped, not like normal permanent or deciduous teeth, and suggest to me modification as a result of long association at the side of an expanding premolar. Further, the general evidence obtained from rodents and from mylagaulids in particular does not, to my mind, support DORR's contentions.

DORR's argument is not based on homologies, but on the study of the structure of several contemporary or nearly contemporary specimens of similar evolutionary grade. Treating these specimens as a more or less isolated problem in tooth identification, it seems to me that at least three points are worthy of attention. (1) The tooth most directly replaced by $P_4$ should be called $Dp_4$. This is clearly in one example, a specimen of *M. vetus,* the tooth called $Dp_3$ by DORR. In this specimen an unerupted $P_4$ is in the space immediately below and between roots of a deciduous tooth that has been regarded heretofore as $Dp_4$ because of this relationship. (2) If the one certain milk tooth is $Dp_3$, as DORR would have it, then its permanent replacement is suppressed, and the remarkable presence of two lower milk teeth must be recorded. Except possibly in such peculiar cases as the bathyergoids, this is not known to occur in rodents. In many fossil rodents actual specimens having one lower milk tooth, but never two, are known. The upper dentition presents the same problem. Here, according to DORR's thesis, there should be three deciduous teeth, the one commonly identified as $Dp^3$ being $Dp^2$ and so on. But the peglike $P^3$ replaces the deciduous peglike tooth directly (known to do so in *M. vetus*). It seems entirely unlikely that in advanced mylagaulids this tooth should be $P^2$ and in all other primitive rodents that it should be $P^3$. (3) In DORR's formula $M\frac{3}{3}$ are absent in *Mesogaulus* and more advanced mylagaulids. The $M\frac{3}{3}$ are greatly reduced in at least some individuals of *Mesogaulus,* and the terminal tooth in some individuals of *Mylagaulus* seems more reduced than is general in *Mesogaulus*. Thus, it seems possible that the third molars can be lost, as DORR claims. Nevertheless, loss of the third molar in noncarnivorous mammals is rare, and is rare also (although reduction in size is not) in rodents. Further, if *Promylagaulus* has $M\frac{3}{3}$ and *Mesogaulus* does not, then reduction is extraordinarily rapid, for in our specimens of *Mesogaulus* from Quarry A the terminal teeth, $M\frac{2}{2}$ (especially $M^2$), under DORR's theory, are relatively reduced in turn. Moreover, in some advanced and terminal members of the Mylagaulidae (*Mylagaulus?* sp. cf. *M. monodon* of the Rome local fauna, WILSON, 1937, pl. 1, fig. 8) the same dental formula as in *Mesogaulus* is still present, and the most posterior molar no more reduced relative to "$M_1$" than before.

DOWNS (1956, p. 215) has suggested as an item in favor of the DORR formula that otherwise the supposed $M_1$, "would have been first hypsodont, then turned brachyodont (with prominent roots) in its evolutionary history." Actually, it is not necessary to suppose that much reversal ever occurred, but instead that the enlarging $P_4$ prevented the acquisition of much hypsodonty by the tooth along side of it.[13] Measurements actually seem to show that $P^4$, $M^2$, and $M^3$ have all achieved about the same relative hypsodonty. $M^1$ is distinctly less hypsodont than these, but more hypsodont than $Dp^4$, perhaps resembling slightly more the other permanent teeth than it does $Dp^4$, although being nearly halfway between.

In summary, starting with the assumption that the $M_1$ of authors equals $Dp_4$, the DORR theory then requires two circumstances (presence of two lower deciduous teeth, and loss of $M_3$), neither of which would be expected in Miocene rodents.

Parenthetically, I think one is inclined to make too much of the distinction between the molars and the deciduous dentition. It is reasonable to assume that the permanent dentition consists of two quite different items: (1) the incisors, canines, and premolars, which constitute, generally, a genuine second set of teeth, and (2) the molars which are part of the deciduous set but with delayed eruption. This delay in eruption varies considerably, and $M\frac{1}{1}$ in many primitive mammals appears significantly before $M\frac{2}{2}$. A tooth in the position of $M_1$ which does not, nor historically (at a mammalian level) never did, have a successor is a molar regardless of structure. In the present case, there is only one replacement tooth involved for two teeth in the first series. In *M. vetus* this replacement forms beneath what has been called $Dp_4$. The tooth behind should be termed a molar until such time as evidence of an historical nature is available to show suppression of the permanent replacement. In other words, it seems to me that although DORR's interpretation may conceivably be correct, in the absence of some historical evidence that it is, we are obliged to retain the orthodox solution. Conversely, I think there is considerable phylogenetic evidence to in-

[13] Regardless of theory, in the upper molars of *M. paniensis,* $M^2$ (or $M^1$ of DORR formula) is approximately twice as high-crowned as $M^1$ on the internal tooth margin, and 38 percent higher-crowned externally, if comparison of specimens with comparable stages of wear of pattern are made. [The extreme limit in the available sample is 110 percent and 66 percent respectively; it should be noted also that $M^2$ is only slightly larger than $M^1$.] $M^1$ is slightly shorter-crowned (absolutely) than $M^3$, but the former tooth has about 2.5 times the cross-sectional area. $M^2$ has about 3 times the area of $M^3$, but is only 30 percent higher-crowned externally, and 58 percent internally.

dicate that the formula given by MATTHEW and most others is the correct one, and it is here in this area that I, myself, find the greatest difficulty in accepting DORR's formula.

The aplodontids, represented today by the sewellel, are certainly closely related to the mylagaulids, and their common ancestry, if not to be found in *Meniscomys,* can not be too far removed temporally or structurally from this genus. $Dp^4$ of *Liodontia alexandrae* (Aplodontidae, middle Miocene) is so close to $Dp^4$ of *Mesogaulus paniensis* as to leave not only no doubt as to the close relationship between mylagaulids and aplodontids, but also no doubt that the two teeth are homologues. In *Liodontia,* the three teeth behind $Dp^4$ are all hypsodont and permanent in the jaw. Moreover, a tooth by tooth comparison can be made between the upper dentition of *M. paniensis* and that of *Meniscomys hippodus* as figured by MCGREW (1941, fig. 7). Assuming a traditional formula, a close resemblance in pattern between each of the five teeth ($P^3$, $P^4$, $M^1$-$M^3$) of *Mesogaulus* and corresponding ones of *Meniscomys* can be seen. Only in the rather thin enamel in places, and the somewhat anteroposteriorly extended outline of $M_1$ is there any suggestion that "milk" teeth are involved. In *Meniscomys,* as in all aplodontids and related paramyines, the accepted dental formula is $\frac{1.0.2.3}{1.0.1.3}$, with two upper and one lower deciduous teeth in all known cases. It is difficult to see how the ancestral aplodontid dentition evolved into that postulated by DORR for *Mesogaulus* without leaving more evidence than is available for the DORR formula. *Promylagaulus* represents an advance over *Meniscomys* toward typical mylagaulids, although in the former only the permanent dentition is known. DORR (1952, p. 324) seemingly accepts the orthodox interpretation of the dentition of *Promylagaulus*—and by inference then that (permanent at least) in the aplodontids. Yet almost certainly, the first cheek-tooth preserved in AMNH10824 (MCGREW, 1941, fig. 3) is the homologue of $M_1$ (DORR's $Dp_4$) in *Mesogaulus paniensis. Mylagaulodon* brings us another step along the mylagaulid path. This genus is represented almost solely by the type specimen of *M. angulatus.* Species of *Mesogaulus* complete a structural line leading to *Mylagaulus.* The first species of the former appears as early as late Arikareean (equals upper Harrison). It is indeed difficult to imagine in looking at the entire series that the peglike $P^3$ of *Promylagaulus* is not homologous with the peglike tooth in *Mesogaulus* and so on. A peglike predecessor of this tooth, as before stated, is known in *Mesogaulus vetus,* which must them be $Dp^3$. The milk tooth predecessor of the enlarged premolar must be $Dp^4$, and the tooth behind it the first molar, unless we are in error in regard to the basic formula in primitive rodents, which I take it is not what DORR contends. $M^1$ finds its counterpart in the lower dentition in the tooth that DORR identifies as $Dp_4$: the latter must be $M_1$ as stated by MATTHEW.

Lastly, examination of such a structural sequence as that figured by STEHLIN & SCHAUB (1951: *Meniscomys,* fig. 486; *Promylagaulus,* fig. 490; *Mesogaulus,* fig. 491; *"Mylagaulus",* fig. 492) impresses one with the changes, in all the molars, that take place in association with an enlarging premolar. Both $M_1$ and $M_2$ in the mid-Pliocene *"Mylagaulus"* have a shape and pattern in the young dentition strongly reminiscent of the heavily worn stages of these teeth in the older species preceding the shedding of "$M_1$." There is, moreover, some evidence that $M_2$ in this kind of Pliocene mylagaulid is also shed, thus completing for $M_2$ at a later date the sequence of events that has made for such a peculiar $M_1$ in *Mesogaulus.* BLACK & WOOD (1956, p. 682) are inclined to favor the DORR theory that in this example the $M_3$ rather than $M_2$ has been lost. Although possibly so, I do not think the evidence marshaled to date goes much toward proving it.

## Family SCIURIDAE

Three sciurid species are tentatively recognized, and arranged in two genera. One of these is a chipmunklike species, which I am assigning questionably to *Palaeoarctomys.* This may be a mistaken assignment, but the alternative of tentative reference to *Tamias* is equally dubious, and apt to be misleading to students of Recent mammals. The other two species are assigned to *Sciurus* in the general sense used by many other workers.

### PALAEOARCTOMYS? BRYANTI Wilson, n.sp.

Figures 60-62, 67

*Sciurus* sp., GALBREATH, 1953 (p. 98).

This species is named in honor of Dr. MONROE D. BRYANT in recognition of his work on North American Sciuridae.

*Holotype.* Right lower jaw bearing $P_4$-$M_3$, crushed but essentially complete, No. 10149, Univ. Kansas Mus. Nat. Hist.

*Referred specimens.* KU9290, an incomplete right lower jaw with $P_4$, $M_2$-$M_3$; KU10150-KU10154, isolated lower cheek-teeth; KU10155-KU10160, isolated upper cheek-teeth. KU10161-KU10162, isolated incisors.

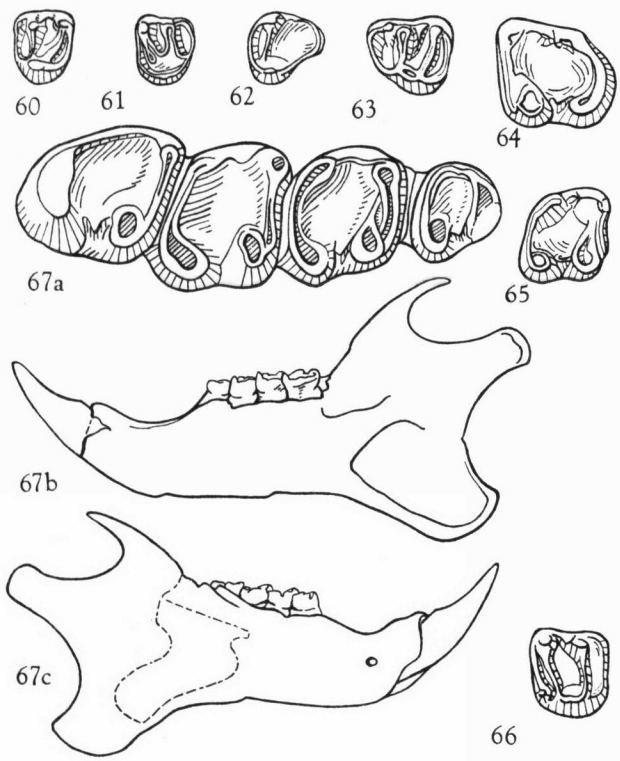
*Geological age and locality.* Sandy silts of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Diagnosis.* Size small (alveolar length $P_4$-$M_3$, 7.1-7.5); essentially brachydont cheek-teeth; cheek dentition relatively light; protoloph and metaloph of upper molars convergent to protocone, metaconule absent as a discrete cusp; lower incisor compressed with multiple, longitudinal grooves; $P_4$ small, relatively short and broad; lower molars with entoconids weak to absent; inner half of $M_2$ notably shorter than outer half; lower jaw relatively heavy and diastema short, with rather shallow diastemal depression; angular process short, rather bluntly terminated, only moderately twisted inwardly.

*Description.* Material of this species is fragmentary, for it is represented only by two lower jaws (one somewhat crushed, the other incomplete), and a number of detached cheek-teeth and incisors. Nevertheless, upper teeth are known which can be associated with the lower dentition with fair confidence, and this circumstance is somewhat unusual in the American Miocene.

Several isolated upper incisors (KU10161) seem referable to *P. ? bryanti*. Except for lesser size, they hardly are separable from those of the European *Sciurus feignouxi* available for comparison.

The fourth upper premolar is not certainly identifiable. KU10157, a right upper cheek-tooth probably is a premolar, and if so is then to be assigned to *P.? bryanti* on the basis of appropriate size. This tooth is oblong and has rounded edges. The crests are relatively large, and the intervening valleys crowded. Only a small parastyle area is present. Protoloph and metaloph converge and unite with the rather anteroposteriorly extended protocone. A faint demarcation on the metaloph seems to represent the metaconule, but this may be more a matter of wear than of the real presence of a cuspule. A second tooth, KU10155, is smaller than KU10157, and more triangular in outline because of a more constricted protocone and a more expanded parastyle. There is no indication of a metaconule, and, as in KU10157, the protoloph and metaloph converge upon, and unite with, the protocone. If KU10155 is not a $P^4$ of *P.? bryanti* it could represent $M^1$ in *Sciurus* species B, to be described below. One, or both of these specimens seemingly is $P^4$ of *P.? bryanti*. In either case, the $P^4$ is smaller than the molars, but has the same general shape. In addition, the lophs are convergent on the protocone, the metaconule obscure or absent, and the parastyle small.




FIGURES 60-67. *Palaeoarctomys? bryanti* (Figs. 60-62) and *Sciurus* sp. A (Figs. 63-66).————60, Left $P^4$, KU10157.————61, Right $M^1$ or $M^2$, KU10158.————62, Left $M^3$, KU10160.————63, Left $P^4$, KU10163.————64, Left $M_3$, KU10169.————65, Right $M_1$, KU10168.————66, Right $M^1$ or $M^2$, KU10165.————67, Type specimen, right lower jaw with $P_4$-$M_3$, KU10149; 67a, occlusal view of $P_4$-$M_3$; 67b, medial view; 67c, lateral view. [Figs. 60-66, ×4.5; Fig. 67a, × 9.5; Figs. 67b,c, ×2.25.]

KU10156 is probably the deciduous upper premolar of *Palaeoarctomys? bryanti*. This tooth has notably divergent roots, and is of an appropriate size and shape. [The only alternative is that it represents the permanent premolar of *Sciurus* sp. B.] This triangular tooth has considerable development of the parastyle, and is unlike the molars in general shape. A fairly distinct metaconule is present, as well as a robust mesostyle; the latter is absent in KU10155, but present in KU10157.

Presumably $M^1$ is smaller than $M^2$, but this presumption was the basis for tentative separation, and these two molars, KU10158-KU10159, will be described together. They are brachydont to submesodont, and subtriangular in shape. The paracone and metacone are prominent, and by comparison, the inner halves of the protoloph and metaloph are subdued, but these crests in fact are well-developed. The protoloph is oriented at right angles to the anteroposterior axis of the tooth. The metaloph is at an angle to the axis, and consequently the two lophs converge toward the protocone to which they are both united. A metaconule is not, or barely, evident even on unworn crowns. Mesostyles are present, and the parastyle shelf is fairly prominent, for example in KU10158.

The third molar KU10160 has its talon somewhat expanded, but so far as can be seen, no structure (metaloph) exists within the basin. The curving posterior rim seems also without tuberculation.

In the specimens of the upper dentition, a slight tendency exists for them to fall into more *Sciurus*-like and more *Citellus*-like divisions, but I think this can probably be ascribed to stages of wear together with some individual variation in characters, and I am not regarding it as nomenclaturally significant. A lesser tendency may also be present in the lower dentition.

The lower jaw is represented by KU10149, a nearly complete but somewhat crushed right lower jaw, and KU9290, uncrushed but with little other than the body of the jaw remaining, also a right jaw. If it is legitimate to unite these two specimens in a single species, then

almost all features of the lower jaw may be ascertained. It is, on the whole, quite like that of a chipmunk *(Tamias),* save in its over-all larger size, and its greater depth beneath the tooth row. Thus, the diastemal part of the mandible is relatively slight and the diastema of moderate length; and the anterodorsal border of the diastema is slightly above the level of the alveolar border. The large mental foramen is situated midway between $P_4$ and incisor. The condyle is so placed that it is not much above the level of the tooth-row, and the angular process does not extend so far posteriorly as the condyle. This process is barely and rather bluntly pointed. The coronoid process is relatively long and slender. It has its origin at about the hinder end of $M_2$. The masseter fossa extends forward to the posterior edge of $P_4$. A large scar in advance of the fossa proper may indicate an attachment for an anterior slip of the *masseter lateralis.* The anterior termination of the fossa is broadly rounded; the ventral crest is much stronger than the dorsal one.

The above characterization departs somewhat from that given by GALBREATH (1953, p. 96-97) who had only KU9290 available. He regarded the jaw as deep and heavy with short diastema, and hence as like that in *Sciurus.* Part of the bony sheath of the incisor is missing, but missing in such a way that the diastemal part of the jaw can be interpreted in two ways. The second specimen, KU10149, is fractured and hence somewhat unreliable, but I think that *P.? bryanti* had less of a *Sciurus*-like diastemal region than GALBREATH thought.

The lower incisor is relatively large (for the size of the cheek dentition) and deep. The ratio of depth to width in KU9290 is approximately two to one; it may be somewhat less in some others. A feature of the incisors, revealed by KU10149, is the multiple grooving of their anterior enamel surfaces. In the type, about six grooves are present running more or less continuously, but slightly anastomosing, toward the tip of the incisor. Such grooves are present in present day marmots, chipmunks, and in *Reithrosciurus.* In KU9290, the incisor is broken off inside the alveolar sheath, and similar grooves can not be traced although at least short furrows can be seen. There is every reason to believe that definite grooves are characteristic of the species, at least in fully adult life. The lower incisors seem to have somewhat more persistent grooving than the uppers on the anterior surface of the enamel, but to be smoother on the lateral surface. Degree of compression is nearly the same, although uppers possibly average higher. On one upper incisor, a rather faint, broad and shallow groove is present, perhaps a precursor of the grooves present in the late Miocene species of *Arctomyoides* and *Palaeoarctomys* (BRYANT, 1945, p. 359, 361).

GALBREATH has described the lower cheek-teeth of *Palaeoarctomys? bryanti* in detail, except for $M_1$, which is missing from KU9290. Observations additional to those recorded by GALBREATH are as follows: (1) $P_4$, relatively small and broad; (2) $M_1$, resembling $M_2$ but slightly smaller, more elongate, and with inner border less shortened; (3) $M_2$, posterointernal edge reduced so as to make a much shorter inner than outer side and to bring the entoconid into an anterior position; anterior

*Measurements of* Palaeoarctomys? bryanti, *in Millimeters*

| | LOWER JAW AND TEETH | | |
|---|---|---|---|
| | KU10149 | KU9290 | Various teeth |
| $P_4$-$M_3$, alveolar length | 7.5 | 7.1 | ..... |
| $P_4$-$M_3$, ap | 6.9 | 6.8 | ..... |
| Diastema, $\underline{I}$-$P_4$ | 6.4+ | ..... | ..... |
| Depth of jaw beneath $M_1$ | 6.0 | 6.4 | ..... |
| Depth of jaw at diastema | 4.4 | ..... | ..... |
| Height of jaw (base of angular process to tip of coronoid) | 15.6 | ..... | ..... |
| Length of jaw (tip of $\underline{I}$ to condyle) | 30.6 | ..... | ..... |
| Ratio of alveolar length to depth of jaw | 1.25 | 1.10+ | ..... |
| Ratio of diastemal length to alveolar length | 0.85 | ..... | ..... |
| Ratio of depth of jaw to diastemal length | 0.93 | ..... | ..... |
| $\underline{I}$, ap | 2.6 | 2.9 | 2.6-, 2.0(a) |
| tr | 1.3 | 1.4 | 1.3, 1.1 |
| ap/tr | 2.00 | 2.07 | 2.0, 1.81 |
| $P_4$, ap | 1.25(b) | 1.5 | 1.25, 1.4 |
| tr | 1.4 | 1.5 | 1.3, 1.4 |
| $M_1$, ap | 1.6 | ..... | ..... |
| tr | 1.9 | ..... | ..... |
| $M_2$, ap | 1.75 | 1.75 | 1.8, 1.8 |
| tr | 2.0+ | 2.1 | 2.0, 2.0 |
| tr/ap | 1.14 | 1.14 | 1.11, 1.11 |
| $M_3$, ap | 2.1 | 2.1 | 2.0 |
| tr | 2.0 | 2.0 | 2.0 |
| tr/ap | 0.95 | 0.95 | 1.00 |
| | VARIOUS UPPER TEETH | | |
| $\underline{I}$, ap | 3.1, 2.7, 2.8 | | |
| tr | 1.4, 1.25, 1.4 | | |
| ap/tr | 2.21, 2.16, 2.0 | | |
| $DP^4$, ap | 1.3 | | |
| tr | 1.4 | | |
| $P^4$, ap | 1.4, 1.5 | | |
| tr | 1.7, 1.8 | | |
| $M^1$, ap | 1.5+, 1.6+ | | |
| tr | 2.0, 2.0 | | |
| $M^2$, ap | 1.7, 1.75 | | |
| tr | 2.2, 2.2 | | |
| $M^3$, ap | 2.2 | | |
| tr | 2.1 | | |

(a) Young specimen.
(b) Broken.

cingulum tending to become separated from the protoconid, but this characteristic not sharply marked in any of our specimens.

A notable feature of the row of cheek-teeth is its relative lightness. The enamel of the basins was probably finely rugose, but this cannot be established positively.

The lower cheek-teeth may be characterized briefly as essentially brachydont, light in respect to either the incisors or jaw; $P_4$ small and relatively broad; trigonids of cheek-teeth rising little above talonid; entoconids weak to absent?; posterolophids more or less curving forward, with the result in $M_2$ of bringing the entoconid forward; $M_3$ relatively short and broad.

*Comparisons.* The following species of the Sciuridae have been named from the North American Miocene: (1) Arikareean, *Sciurus ballovianus, S. vortmani, S. tecuyensis;* (2) Hemingfordian, *Arctomyoides oregonensis, Protospermophilus malheurensis, P. tephrus, P. angusticeps, Citellus ridgwayi;* (3) Barstovian, *Eutamias ateles;* (4) Barstovian?, *Citellus primitivus, Arctomyoides arctomyoides, Palaeoarctomys montanus, P. macrorhinus.* From these, *Palaeoarctomys? bryanti* differs in shorter teeth, excepting *Sciurus ballovianus, Protospermophilus tephrus, Citellus ridgwayi,* and *Eutamias ateles. S. ballovianus* is from an older horizon, and, if measurements usually given are correct (BRYANT, 1945, p. 345), has an actually as well as relatively shorter diastema, and a much heavier dentition in respect to the depth of jaw. In addition, more quadrate upper molars may be present, and the mental foramen of the lower jaw may be more posteriorly placed.

The other three species having tooth rows of comparable length are known only by skulls and upper dentition or upper dentition alone (except an $M_3$ of *Eutamias ateles*), so that comparisons are necessarily limited. They are all distinctly later geologically, the last, *E. ateles,* much so. In the only available specimen of *Protospermophilus tephrus,* the dentition is much worn (GAZIN, 1932, p. 59). It is quite close in size and proportions of the individual teeth to *Palaeoarctomys? bryanti,* but indirect evidence suggests that the cheek-teeth are more robust relative to jaw or skull size. Moreover, on the basis of characters in the skull, *P. tephrus* has been united with *P. malheurensis* and *P. quatalensis* (type species) under the genus *Protospermophilus* (BRYANT, 1945, p. 344). In other species of *Protospermophilus,* the metaloph bears distinct metaconules absent or nearly so in *P.? bryanti. Citellus ridgwayi* (GAZIN, 1932, p. 61) is somewhat larger in its dentition than *P.? bryanti,* and is thought to be more or less allied to such citellids as *Callospermophilus.* This suggests a species considerably more advanced than ours. BRYANT (1945, p. 355) reports that $P^4$ of *C. ridgwayi* seemingly lacks an anterior cingulum. Further, the fact that the incisor stumps preserved in the type of *C. ridgwayi* remain undescribed suggests in negative fashion that they have the smooth enamel typical of citellids.

*Eutamias ateles* (HALL, 1930a, p. 314) is distinctly younger geologically than *Palaeoarctomys? bryanti,* and is somewhat smaller as well.

A number of European sciurid species of the Aquitanian and Miocene structurally resembles *Palaeoarctomys? bryanti.* Especially worthy of mention are: *Sciurus feignouxi* (Aquitanian), *S. costatus wintershofensis,* and *S. fissurae* (Burdigalian), and *S. bredai* (Vindobonian). Save *S. costatus wintershofensis,* they all have larger cheek-teeth than *P.? bryanti* (DEHM, 1950, p. 338), but the noteworthy part about this distinction is that the jaws and incisors are much more nearly of a like size. Hence, *P.? bryanti,* by comparison, is more small-toothed. They also differ in lesser reduction of the posterinternal border of $M_2$, generally more elongate $P_4$, and many other more minor points, but broadly they are at the same stage of evolutionary development (with the probable exception of *S. costatus wintershofensis*). I would assume, however, that *S. bredai* is slightly more advanced on the whole, *S. costatus wintershofensis* more primitive, and *S. feignouxi* and *S. fissurae* about comparable although possibly more primitive. In all, there is a mingling of characters that are seemingly primitive with those that are advanced so that such evaluations become difficult to make. Especially is this true with some features that are ambiguous in regard to evolutionary stage.

Generic assignment of the Colorado species is difficult. Early Miocene species in North America and Aquitanian species in Europe as well as most of the Burdigalian species have been referred only to *Sciurus.* European practice is to include almost all fossil species of sciurids in living genera. *Paracitellus* DEHM (1950) of the Burdigalian, if it is a sciurid, forms a rare, recent exception. In North America, on the other hand, several of the post-Arikareean sciurids are placed in extinct genera, and little post-Arikareean material is assigned to the tree-squirrels. Two different taxonomic scales seemingly are involved for the later Miocene as between North America and Europe, and as between early and late Miocene on both continents. By European standards, *Palaeoarctomys? bryanti* should be assigned to *Sciurus.* By American standards, *Sciurus bredai* is a ground squirrel and not of the genus *Sciurus.* It is not likely that any of the early Miocene species are really *Sciurus* in a strict sense. There is, however, a real difficulty in working with fragmentary sciurid material that has produced at times a too conservative European approach, and at times an impractical American one. A possible solution is to revive such a name as *Palaeosciurus* POMEL (1852) as a wastebasket for those primitive species that are essentially at a tree-squirrel level of evolution (it is not clear to me that the type species of *Palaeosciurus, P. feignouxi* really is) and a comparable name for rather

*Comparative Measurements of* Sciuridae

| | *S. c. wintersi-hofensis* | *S. fissurae* | *S. bredai* | *A. oregonensis* | *Palaeoarctomys? bryanti* | *Arctomyoides arctomyoides* | *Palaeoarctomys montanus* | *Palaeoarctomys macrorhinus* | *Marmota mexicana* | *Sciurus fergnousi* | *Sciurus ballovianus* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Alveolus length / Jaw depth | 1.32 | 1.45 | 1.52+ | 1.40 | 1.10+-1.25 | 1.36 | 0.95 | — | 1.49 | 1.38 | 1.55 |
| Diastema length / Alveolus length | — | 0.66 | 0.85 | 0.88 | 0.85 | 0.81 | 1.18 | — | 0.67— | 0.73 | 0.42 |
| Jaw depth / Diastema length | — | 1.03 | 0.76 | 0.80 | 0.93 | 0.89 | 0.88 | — | 1.0 | 0.98 | 1.50 |
| Jaw length / Alveolus length | — | 3.7 | — | — | 4.08-4.31 | — | 4.5 | — | — | — | ?2.14 |
| $\frac{\overline{I}, ap}{tr}$ | 2.66-2.87 | 2.0 | 1.84 | 1.85 | 2.00-2.07 | 1.75 | 2.08 | — | 1.82 | 2.0— | — |
| $\frac{P_4, ap}{tr}$ | 1.33 | 1.05 | 1.0+-1.16 | 1.08 | 0.9-1.00 | 1.00 | 0.86 | — | 1.02-1.05 | 1.11 | — |
| $\frac{M_1, ap}{tr}$ | 1.30+ | 0.87 | 0.87-0.95 | 0.85 | 0.84 | 0.83 | 0.85 | — | 0.89-0.94 | 0.95 | — |
| $\frac{M_2, ap}{tr}$ | 1.06 | 0.92 | 0.90 | 0.94 | 0.83-0.87 | 0.86 | 0.76 | — | 0.92 | 0.88 | — |
| $\frac{M_3, ap}{tr}$ | 1.18-1.23 | 1.08 | 1.20 | 1.40 | 1.05 | 1.05 | 1.07 | — | 1.05 | 1.08 | — |
| $\frac{Dp^4, ap}{tr}$ | — | — | 1.00 | — | 0.92 | — | — | — | — | — | — |
| $\frac{P^4, ap}{tr}$ | — | 0.75-0.84 | 0.83 | — | 9.82-0.83 | 1.03 | — | 0.92 | 0.93 | — | — |
| $\frac{M^1, ap}{tr}$ | 1.00 | 0.83-0.91 | 0.86 | — | 0.75-0.80 | 0.88 | — | 0.90 | 0.84 | — | 0.93 |
| $\frac{M^2, ap}{tr}$ | — | 0.84-0.89 | 0.83 | — | 0.77-0.79 | — | — | 0.88 | 0.86 | — | — |
| $\frac{M^3, ap}{tr}$ | 1.12 | 1.00-1.17 | 1.02 | — | 1.04 | — | — | 1.00 | 0.94 | — | — |
| $\frac{I, ap}{tr}$ | — | 1.78-2.08 ? | — | — | 2.0-2.21 | 1.53 | 1.60 | 1.37 | — | — | — |

generalized members of the ground-squirrel group. I am not in a position that would warrant formal proposals. Consequently, as an expedient, I am recognizing what seems to me to be the vague beginnings of a recognizable split between tree-squirrels and ground-squirrels in the Quarry A fauna by assigning part of the material to *Sciurus (s.l.),* and *P.? bryanti* tentatively to a genus that has marked ground-squirrel characters in its later members.

BRYANT (1945) has listed the characteristics of tree-squirrels as contrasted with those of terrestrial squirrels (ground squirrels, chipmunks, and marmots). If one makes use of his criteria, it would seem that the Quarry A species, *Palaeoarctomys? bryanti,* is in the terrestrial squirrel group. If, however, the paramyines are in fact ancestral to the sciurids,[14] I think it is possible to reduce the list considerably by removal from it of those characteristics assuredly present in the assumed ancestry. Thus the most concrete evidence, but not the only evidence (for the dismissed features collectively are suggestive) for placing *P.? bryanti* with the terrestrial squirrels is: (1) the reduced entoconid area in $M_2$, and (2) the relatively low position of the condyle. If we are able on basis of the above-mentioned features to assign *P.? bryanti* to the ground-squirrel, marmot, chipmunk division, then the evidence favors relationship to either the chipmunks or the marmots. Most, if not all, Recent ground-squirrels have smooth incisors (BRYANT, 1945, p. 374).

In favor of a relationship of *Palaeoarctomys? bryanti* to the chipmunks are: (1) angular process relatively short; (2) lower incisors with longitudinal grooves of moderate persistence; (3) mesostyles present, mesoconids present?; and (4) metalophs complete on $M^1$ and $M^2$. Opposed to assignment of *P.? bryanti* to the chipmunks are the following observations: (1) *P.? bryanti* differs from *Eutamias* and *Tamias* in a number of morphological details, such as heaviness of lower jaw

[14] I am strongly of this opinion. It should be pointed out, however, that SCHAUB (STEHLIN & SCHAUB, 1951, and elsewhere), for example, thinks the sciurids to be without known ancestors, if I interpret him correctly.

and relatively short anteroposterior diameters of molars $M\frac{1-2}{1-2}$; (2) chipmunks may not in themselves be a natural group (WHITE, 1953, p. 560); (3) characters most strongly suggesting assignment of *P.? bryanti* to chipmunks would also suggest chipmunk affinities for several of the European Miocene species and it is hardly likely that these all are chipmunks.

What seems most evident is perhaps not a relationship to the chipmunks (nor to the marmots, for that matter), but to certain North American fossil squirrels, namely *Arctomyoides oregonensis, A. arctomyoides, Palaeoarctomys montanus,* and *P. macrorhinus.* The two genera *Arctomyoides* and *Palaeoarctomys* are regarded by BRYANT (1945, p. 384) as more closely related to each other than either is to other squirrels. DOWNS (1956, p. 219-220) states that they are closely related, but generically distinct. It seems to me that their generic separation is open to question because they are, or could be, of the same geologic age, and *Arctomyoides arctomyoides* is known only by a rather young, and *Palaeoarctomys montanus* by a fairly old individual. The difference in ontogenetic age undoubtedly accounts for some differences in proportions between the two type species. Be that as it may, BRYANT's chart (p. 384) suggests a common ancestor at about the time *P.? bryanti* lived. With both *Arctomyoides arctomyoides* and *Palaeoarctomys* spp., there is a remarkable agreement in proportions of jaws and teeth. The chief disagreement is in the considerably greater compression of the upper incisors in *P.? bryanti* than in the late Miocene *Arctomyoides* or *Palaeoarctomys. P.? bryanti* resembles *Palaeoarctomys* spp. in possessing relatively small teeth in proportion to the size of the jaw. Small teeth seem not to be an ancestral trait in the Sciuridae. *Palaeoarctomys* is described as having incisors with many longitudinal striations on the incisors, and with two or more distinct grooves on the uppers. The longitudinal striations are coarse in the upper incisors of *P. montanus. Arctomyoides* is described as possessing lower incisors which are finely striated on the anterior surfaces. This suggests a less advanced stage than in *P.? bryanti.* In pattern of the cheek-teeth there is considerable agreement between *P.? bryanti* and *Arctomyoides oregonensis.* $M_3$ is relatively more elongate in *A. oregonensis* than in *P.? bryanti* (and than in the others as well), which may also be taken as a less advanced feature in a somewhat younger species. Finally, the anteroposterior diameter of $P^4$ of *A. arctomyoides* is relatively greater than in either *Palaeoarctomys* or *P.? bryanti.* Chiefly with the above features in mind, I am referring the Colorado species tentatively to *Palaeoarctomys* rather than to *Arctomyoides.*

Such a European species as *Sciurus fissurae* (DEHM, 1950, p. 341-347) may be on essentially the same level or stage of organization as *Palaeoarctomys? bryanti,* but has a more robust dentition, a slightly narrower $P_4$, a masseteric fossa that terminates abruptly under $M_1$, the anterior end of the jaw slightly below the alveolar level, and an $M_2$ lacking the contraction of the inner half. *Sciurus bredai* (La Grive-St. Alban; *S. spermophilinus, fide* DEHM, p. 346) differs from *P.? bryanti* in relatively heavier dentition, less contracted inner half of the $M_2$, better defined (more continuous) grooves (3 or 4) on the lower incisor, more pointed and more distinctly twisted angular process of the lower jaw, less compressed lower incisor, and relatively more elongate $M_3$. I judge *S. bredai* to be structurally similar to, but more advanced than, *P.? bryanti.*

**SCIURUS sp. A**

Figures 63-66

Sciurid sp., GALBREATH, 1953 (p. 97).

Several isolated teeth from Quarry A are of a sciurid distinctly larger than *Palaeoarctomys? bryanti.* KU10163 and KU10164 are assumed to represent the fourth upper premolar. Possibly these teeth are deciduous molars instead. The roots of one are somewhat divergent, and on the other, and more worn one, are broken away (or absorbed) leaving an open base. Other than in this, the teeth appear to be of the permanent dentition. An alternative is that KU10163 represents $P^4$, and the slightly smaller KU10164 represents $Dp^4$. The crown of KU10163 is unlike that of the molars in shape for a large parastyle and anterior valley imparts a triangular outline to the tooth. The lophs are convergent, united to the protocone, and rather strong. No protoconule is present, and the metaconule is obscurely defined. A wedge-shaped mesostyle and a small cuspule immediately behind the parastyle are additional features. The posterior valley is narrow. KU10164 is not only slightly smaller, but its parastyle and mesostyle are less prominent, and the secondary cuspule behind the parastyle can not be seen. Perhaps these teeth, more than the others assigned here, suggest a marmotlike squirrel.

KU10165 and KU10166 are either first or second upper molars, the latter considerably more worn than the former. The lophs are convergent with no trace of the conules. A prominent feature of the crown is the relatively large parastyle area. On the contrary, the mesostyle is small. A swelling at the lingual end of the posterior cingulum may be described as a small hypocone. Nothing is contributed by the worn KU10166, except that its parastyle seems less developed.

KU10167 is a compressed lower incisor having distinct furrows on both the anterior and external enamel surfaces; these furrows almost become grooves at times. The furrows are comparable in development to those in *Sciurus feignouxi,* and seem to be less prominent than in *Palaeoarctomys? bryanti.* They appear to be better developed on the lateral surface than in the latter species.

A moderately worn first or second lower molar, probably the former, KU10168, is present. A fragment of a comparable tooth in unworn condition supplements this

tooth considerably. The cusps are fairly low and plump. The floor of the basin is finely rugose. An anterior cingulum is separated from the protoconid by a shallow notch. A short metalophid that almost reaches the metaconid in KU10168 (distinctly shorter in the fragment) is present, as are mesoconids and mesostylids. An entoconid terminates a posterolophid that lacks much of the curvature seen in *Palaeoarctomys? bryanti*. The hypoconid may be slightly larger than the protoconid.

A third lower molar, KU10169, is a relatively short tooth with heavy, curving posterolophid terminating in a small entoconid. A mesoconid and a mesostylid are present. Both KU10168 and KU10169 have essentially brachydont crowns.

*Measurements of* Sciurus, *sp. A, in Millimeters*

| Spec. No. | KU10163 | KU10164 | KU10165 | KU10166 | KU10167 | KU10168 | KU10169 |
|---|---|---|---|---|---|---|---|
| $P^4$ | | | | | | | |
| ap | 2.5 | 2.3 | ..... | ..... | ..... | ..... | ..... |
| tr | 2.3 | 2.25 | ..... | ..... | ..... | ..... | ..... |
| 1/w | 1.08 | 1.02 | ..... | ..... | ..... | ..... | ..... |
| $M^1$ or $M^2$ | | | | | | | |
| ap | ..... | ..... | 2.4 | 2.4 | ..... | ..... | ..... |
| tr | ..... | ..... | 2.8 | 2.8 | ..... | ..... | ..... |
| 1/w | ..... | ..... | 0.85 | 0.85 | ..... | ..... | ..... |
| $\bar{I}$ | | | | | | | |
| ap | ..... | ..... | ..... | ..... | 4.25 | ..... | ..... |
| tr | ..... | ..... | ..... | ..... | 2.0- | ..... | ..... |
| 1/w | ..... | ..... | ..... | ..... | 2.12 | ..... | ..... |
| $M_1$ or $M_2$ | | | | | | | |
| ap | ..... | ..... | ..... | ..... | ..... | 2.5 | ..... |
| tr | ..... | ..... | ..... | ..... | ..... | 3.0- | ..... |
| 1/w | ..... | ..... | ..... | ..... | ..... | 0.83 | ..... |
| $M_3$ | | | | | | | |
| ap | ..... | ..... | ..... | ..... | ..... | ..... | 3.5 |
| tr | ..... | ..... | ..... | ..... | ..... | ..... | 3.4 |
| 1/w | ..... | ..... | ..... | ..... | ..... | ..... | 1.03- |

The characteristics of these teeth suggest assignment either to the marmot division or to *Sciurus* in a general sense. If the teeth assigned to $P^4$ really occupy this position in the jaw, they are relatively longer than those of *Palaeoarctomys* and Pliocene *Marmota*. Proportions of the cheek-teeth seem not to differ significantly otherwise from those of *Palaeoarctomys* or *Arctomyoides*. Neither are corresponding teeth of *Sciurus feignouxi* much different (except in shape of $P^4$), but perhaps are slightly more primitive on the whole than those of the Quarry A species.

There are a number of differences between species A of *Sciurus* and *Palaeoarctomys? bryanti*,[15] and those differences suggest that the two species are not of the same genus.

[15] Some are: (1) triangular shape of $P^4$ in *Sciurus* sp. A; (2) less striated incisor, but with furrows extending to external surface; (3) larger size; (4) small hypocone on $M^1$-$M^2$.

**SCIURUS sp. B**

Three isolated teeth (see measurements) seem too small for reference to *Palaeoarctomys? bryanti*, and are otherwise slightly more *Sciurus*-like in character. If these teeth do pertain to a single species perhaps a reference to *Sciurus* is more justifiable than any other.

*Measurements of* Sciurus *sp. B, in Millimeters*

| Specimen | KU10170 left $M^2$ | KU10171 right $M^3$ | KU10172 right $M_1$ |
|---|---|---|---|
| ap | 1.6 | 1.7 | 1.5 |
| tr | 1.8 | 1.7 | 1.6- |
| ap/tr | 0.88 | 1.00 | 0.93 |

$M^2$ is more or less quadrate in outline, low-crowned, and lacks conules and mesostyle. The lophs are low and converge upon, and unite with, the anteroposteriorly extended protocone. A large anterior valley is present. The posterior cingulum and valley are not well developed except near the internal side where the cingulum is expanded into a small, but definite, hypocone.

$M^3$ is greatly worn; the heel area is small compared with that in *Palaeoarctomys? bryanti*.

$M_1$ has the metaconid somewhat damaged and its relative height cannot be determined. Otherwise, the tooth has a protoconid seemingly smaller than the hypoconid, and separated from the anterior cingulum by distinct notches. The metalophulid is short and fails to reach the metaconid. A mesostylid is present. The mesoconid is weak and marginal, and of double structure, a feature of the tree squirrels according to BRYANT (1945, p. 288). The more or less curving posterolophid terminates in an entoconid.

These teeth differ little from those of *Palaeoarctomys? bryanti*, but the double mesoconid, more quadrate shape of $M^2$, brachydont crowns and subdued crests seemingly suggest a primitive member of the tree-squirrel group.

**REMARKS ON FOSSIL SCIURIDAE**

BRYANT (1945) in his "Phylogeny of Nearctic Sciuridae" collected data from three sources: (1) Recent Sciuridae, utilizing American squirrels almost exclusively; (2) American fossil sciurids; and (3) the paramyine rodents, for he assumed that those rodents are ancestral to the Sciuridae. Understandably, he put his emphasis on the Recent species in his classification (and hence phylogeny), and the fossils were simply made to fit. He also drew from the same three sources of data to divide characters of the sciurids into primitive (paleotelic) and cenotelic ones. For the most part, *Sciurus* seems to have been regarded as embodying all the characteristics shown by tree squirrels, and to be also a sort of living fossil in respect to the Sciuridae as a whole. It seems almost certain that BRYANT's field of operation was too restricted to permit more than tentative acceptance of his phylogenetic conclusions.

As deficiencies it may be mentioned that: (1) the oldest North American material of any completeness then know nwas not examined by BRYANT (*S. ballovianus, S. vortmani,* from John Day deposits, early Miocene); (2) no Old-World fossil material was studied and in the case of *Marmota, Eutamias, Citellus, Sciurus,* and *Glaucomys* this is an important omission[16]; (3) Old-World Recent species were only casually covered, and it is difficult to apply characters of *Sciurus* to all the Old-World tree squirrels for example; and (4) among paramyines, probably only *Paramys* was studied. BRYANT personally examined only two fragmentary specimens of an age older than the Skull Spring local fauna (late Hemingfordian or early Barstovian) and was misinformed concerning the age of one of these (sciurid? sp. from the Whitneyan). The correspondence in stage of evolution of the Colorado material with the European suggests that no satisfactory phylogenetic study can be made of North American sciurids without careful study of the Old-World species.

Most American students of fossil rodents hold to the view that the paramyine rodents are ancestral to the Sciuridae. SCHAUB (1953, p. 35), among the European workers, has emphatically rejected this relationship. Personally, I am convinced of the correctness of the American point of view. In addition to what I have myself seen, evidence available to A. E. WOOD, who is now reviewing the paramyines, has convinced him of the same thing. In the discussion below, the paramyine theory is accepted, and this leads to some conclusions that might be, but not necessarily would be, modified by the rejection of the theory.

There has been universal acceptance of certain Aquitanian rodents as squirrels. The earliest known sciurids are probably pre-Acquitanian (and pre-Chattian, if there is a difference), but Oligocene. Representative of these are *Cedromus* (WILSON, 1949; GALBREATH, 1953), of North America (Orellan), and *Sciurus* spp., from the phosphorites of France. These species might be interpreted as still not up to the sciurid level, hence advanced paramyines, if one believes in the paramyine theory, or more surely as sciurids if one favors some other origin. Fragmentary specimens could be prosciurine, distinguished with difficulty because of their fragmentary condition from the Sciuridae. In any case, the specimens give a quite incomplete view of what sciurids were like anatomically in the Oligocene.

There are some differences between *Cedromus* and, for example, one of the French sciurids (*Sciurus* sp., British Museum N.H. No. 7463) available to me for comparison. It seems, nevertheless, that No. 7463 is closer to *Cedromus,* although not referable to this genus, than to *Sciurus.* The principal distinctions from *Cedromus* are, in the French species: (1) slightly more anterior position of masseteric fossa; (2) more compressed lower incisor; (3) slight concavity (rather than straight) to diastemal profile; and (4) various minor features of the dentition. Since even among the later squirrels there is variation in the development of the musculature, I think that the most significant difference is in the compression of the incisor, wherein *Cedromus* resembles the paramyines, and No. 7463 (*Sciurus* sp.) resembles most, if not all, squirrels of the early Miocene.

Study of the limited Oligocene material, together with the evidence obtained from the paramyines and the Aquitanian and early Miocene sciurids, suggests that in the typical Oligocene, sciurids generally had the following features (attention is given principally to those features apt to be present in representative fossil specimens).

*Lower Dentition.* (1) Incisors furrowed but without definite grooves, degree of compression ranging from about 1.6, the upper limit of paramyines, to 3.0. (2) Cheek-teeth somewhat elongate, especially $M_3$. (3) Entoconids, mesoconids, and mesostylids more or less distinct. (4) Anterior cingulum possibly tending to be separated from protoconid. (5) Crowns lows, with trigonids low, but not so low as in some tree squirrels. (6) Posterolophids curving. (7) $P_4$ relatively long, but with close-set protoconid-metaconid cusps.

*Mandible.* (1) Masseteric fossa terminates under $M_1$, usually with a prefossa scar area in advance of true fossa (for slip of masseter muscle?). (2) Diastema, $\overline{I}$-$P_4$, short. (3) Dorsal outline of diastemal collar straight to only slightly depressed; anterior end of jaw not much below or above alveolar level. (4) Masseteric fossa rather deeply cupped.

*Upper Dentition.* (1) Metaloph ?not connected to protocone, with distinct metaconule, but no protoconule, protoloph and metaloph converging. (2) $P^4$ similar to molars in shape, lacking prominent parastyle. (3) $P^3$ peglike. (4) Heel on $M^3$ large (variously developed). (5) Upper molars subquadrate.

*Skull.* (1) Braincase not so inflated as in Recent sciurids. (2) Bullae less inflated than in Recent sciurids, and paroccipital processes standing away from bullae. (3) Auditory bullae ossified and strongly attached. (4) Basicranial-facial axis bent. (5) Palate broad.

Evidence obtained chiefly from the paramyines suggests that the following additional characters could be expected in the sciurid ancestry, and that their presence in a modern sciurid is to be regarded as a retention: (1) angular process of lower jaw of moderate size and little twisted; (2) condyle of lower jaw high above toothrow; (3) enamel of cheek-teeth rugose; (4) ?hypoconids larger than protoconids in molars; and (5) lower jaws relatively high and short. This list resembles one given by BRYANT (1945, p. 365-367), amplifying BRYANT's somewhat, but also contradicting it in one or two characters. In any case, the list is based on paramyines and Oligocene-early Miocene sciurids not covered by BRYANT.

Early Miocene species seem all to have (1) moderately deep lower incisors (ratio 2.0 upward); (2) furrowed incisors with furrows becoming increasingly prominent as grooves; and (3) converging upper molar crests without distinct conules. Certain much later ground-squirrels have relatively wide lower incisors, and distinct conules

[16] To be exact, BRYANT did consider Old World records (e.g., p. 385 on *Glaucomys*) but there is no evidence that consideration went farther than making note of published generic records of the above.

and disjunct metalophs on the upper molars. It is important to know whether or not these conditions can be secondarily acquired. Changes in proportion of the incisor seem easy to accept, but reappearance of the metaconule is not.

It has been assumed that the early squirrels were arboreal and small. Although this may have been true, it is, I think, also possible that the ancestral type was terrestrial. Certainly a range in size comparable to that of chipmunk to marmot seems to have existed at several levels stratigraphically: (1) among paramyines, in the late Eocene of California (WILSON, 1940); and (2) among sciurids, in the Chattian of Germany (FREUDENBERG, 1941). Apart from the habits of early squirrels, it seems to me in any case that such a squirrel as *Sciurus* has moved away anatomically from an ancestral type about as much as have many existing ground-squirrels, at least in regard to those parts most frequently found as fossils. Last, it is not too clear how in the earlier part of the sciurid record we are to distinguish tree-squirrels from ground-squirrels on the basis of fragmentary specimens, although I have attempted to do so on earlier pages. A number of the characteristics that have been used to distinguish *Citellus*-like from *Sciurus*-like species in the fossil record simply are primitive features signifying little except the latter fact.

Probably no Oligocene or early Miocene sciurid represents *Sciurus* in a strict sense. In North American Miocene sciurids, seven of the 12 species are known by more than ramal fragments or dentitions. Of these seven, five are referred to extinct genera, and one of the remaining two *(Sciurus ballovianus)* has not really been studied taxonomically since COPE's day. Of the five known only by the above mentioned parts, only one, *Arctomyoides arctomyoides,* is assigned to an extinct genus. The inference is fairly plain, that possession of complete material would eliminate reference of any of these specimens to an existing genus. Probably one of the abandoned old names such as *Palaeosciurus* POMEL eventually will be revived for several species now referred to *Sciurus,* as previously mentioned.

To focus attention on the hazard of relying on an established determination in the literature, it is pertinent to describe such a European species as *Sciurus bredai* [=*S. spermophilinus*] of the La Grive-St. Alban fauna. DEPERET was hardly able to distinguish this species from Recent *Sciurus*. FORSYTHE-MAJOR (1893, p. 191), however, pointed out several features which showed *S. bredai* to be distinct, but still he thought the species was a tree squirrel, and continued to refer it to *Sciurus*. According to characters used by BRYANT (1945, p. 369-370), this species is clearly a ground squirrel of some kind. Characters shown by *S. bredai* are: (1) infraorbital canal narrowly oval in outline, tubercle for *M. l. superficialis* immediately ventral to it, hence in advance of $P^4$, and partly on ventral surface of rostrum, partly on lateral surface; (2) paired rostral depressions behind incisors for muscles of cheek-pouches; (3) somewhat basined dorsal termination of zygomatic plate ending with slight crest and scar; (4) convergent metaloph and protoloph, without conules usually, uniting with protocone; (5) $P^4$ shaped like $M^1$-$M^2$; (6) mandible relatively shallow diastema relatively long; (7) anterodorsal edge of jaw at level of alveolus or slightly higher; (8) angular process of jaw more pointed than in *Palaeoarctomys? bryanti,* and more twisted internally; (9) entoconids of lower molars absent to obscure; (10) lower molar basins moderately deep; (11) posterolophids curving, uniting with mesostylids in some specimens and reaching nearly to bases of metaconids; (12) $M_3$ moderately lengthened; (13) hypoconids and protoconids of nearly equal size; and (14) lower incisors becoming less compressed (ratio 1.84), with three to four pronounced grooves on anterior surfaces.

In addition, *Sciurus bredai* has some primitive characters, or characters of uncertain status, which are seen in a few fossil ground squirrels: (1) "protoconulids" fairly prominent with anterior cingula markedly separated from protoconids (also more or less present in *Protospermophilus quatalensis, Arctomyoides oregonensis*); and (2) masseteric fossa pointed anteriorly, its dorsal crest prominent, dorsal crest having anterior part for separate slip of masseter, fossa proper terminating under posterior part of $M_1$, anterior part under anterior edge of $M_1$ (somewhat as in *P. quatalensis*). Both of these features are perhaps most nearly comparable to those seen in *S. tecuyensis*. The tooth structure, on the whole, markedly resembles that in *A. oregonensis* (see table of ratios). Although about half of the listed characters (4, 5, 7, 10?, 11) may be dismissed as seemingly pertaining to a generalized sciurid, enough remain (1, 2, 3?, 6, 9, 12, 13?, 14 in part) to suggest that *S. bredai* is a primitive ground-squirrel, more or less comparable to various late Miocene citellids of North America, but distinct from them generically.

## Suborder CASTORIMORPHA

I have adopted WOOD's (1955) classification in which the beavers are set apart in their own suborder. Both WOOD and SCHAUB are inclined toward the view that the beavers are related to one or another of the groups formerly associated together under "Hystricomorpha" (Theridomyoidea, Hystricoidea, Caviomorpha). It may be added, lacking a more suitable place, that the time span for European castorids usually given (e.g., WOOD, 1955, p. 175) as late Oligocene to Recent is in error. A lower jaw in the British Museum of Natural History collections is from the lower Hamstead beds of the Isle of Wight. These beds carrying an Oligocene mammalian fauna

are overlain by marine Rupelian, and are no younger than Orellan, probably Chadronian in age (PILGRIM, 1940, p. 10-11). This beaver was identified by STEHLIN as a new species, but seemingly he never published upon it. If of early Oligocene age, as is likely, it is as old as any beaver in North America. The simultaneous appearance of beavers on the two continents would remove one small obstacle to considering the Castoridae as especially related to the Hystricoidea rather than to the Caviomorpha.

## Family CASTORIDAE

Two kinds of beavers are present at Quarry A. The more common is an unnamed species of *Monosaulax,* more primitive than the late Hemingfordian Stewart Spring beavers identified as *M. pansus* by STIRTON (1935, p. 416). It is less certainly more primitive than *M. curtus* (probably Sheep Creek), but chiefly because of the paucity of material for comparison. It almost surely is the most primitive known species of the genus. A rare beaver, represented only by part of the skull, but bearing teeth, and two isolated cheek-teeth, is much larger. Tentatively, it is regarded as an early stage in the *Anchitheriomys* [=*Amblycastor*] phylum.

### ANCHITHERIOMYS? sp.

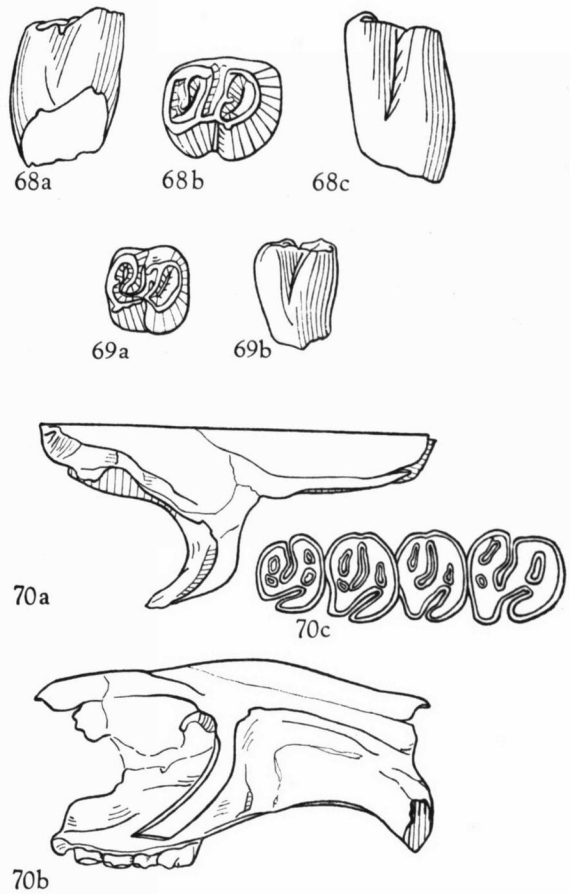
Figures 68-70

A large beaver, much larger than *Monosaulax,* n.sp., described later, is represented by KU10173. This specimen consists of the right half of the skull anterior to the interorbital constriction with $P^4$-$M^3$ and alveolus for the incisor. Only two additional specimens of this species are present in the collection: KU10174, an unworn right upper cheek-tooth (deciduous?); and KU10175, a slightly worn left lower $M_1$ or $M_2$.

So far as published records are concerned, KU10173 represents a species larger than any other known from the North American Miocene save *Monosaulax senrudi, Hystricops venustus,* and *Amblycastor fluminus.* These are all supposed to be of considerably later age, and the latter two certainly are. The Colorado beaver is comparable in size to individuals of *Steneofiber depereti* and *S. jaegeri* of the European Miocene, and the former is perhaps of comparable geologic age. KU10173 shows several characters that ally it with *Steneofiber* rather than with *Monosaulax* or *Palaeocastor.* KU10173 is clearly less advanced than *A. fluminus,* and materials of *Hystricops* are too scanty for comparison. The Quarry A species probably is an ancestral amblycastor *(Anchitheriomys)* but positive evidence for this assignment is lacking at present.

Typical *Palaeocastor* is a beaver with short, wide skull of more or less fossorial modification. *Anchitheriomys?* sp. differs from it, and agrees with *Steneofiber,* in longer, narrower skull, long, posteriorly pointed nasals, and deep rostrum with convex dorsal surface. The root of the zygomatic arch is not so far forward relative to the cheek dentition as in most specimens of *Palaeocastor,* and is on a line with $P^4$. Area of dorsal exposure of the lacrimal seems to be like that in *Steneofiber.* The low boss or knob for attachment of the *lateralis superficialis* muscle resembles that in an immature skull of *Steneofiber* (BM M8155) available for comparison. The only observable difference is that in the BM M8155 the rugosity for attachment of the *M. l. superficialis* is on the lateral surface of the knob rather than on the ventral (and possibly anterior) surface.

The upper cheek-teeth of KU10173 are at least moderately worn. In their present stage of wear they are relatively short, and of the type in which the internal wall is greatly lengthened in comparison with the external




FIGURES 68-70. *Anchitheriomys?* sp.————68, Left $M_1$ or $M_2$, KU10175; 68a, medial view; 69b, occlusal view; 68c, lateral view; ×2.4.————69, Right upper cheek-tooth, KU10074; 69a, occlusal view; 69b, medial view; ×2.3.————70, Skull fragment, right side, KU10173; 70a, dorsal view, ×0.7; 70b, lateral view, ×0.7; 70c, occlusal view right $P^4$-$M^3$, ×1.75

one. The crown height was less than in *Steneofiber depereti,* and approximately (relatively) as in *S. castorinus.* Each cheek-tooth has one internal fold of enamel (hypoflexus), the corresponding groove or stria on the side of the tooth being extremely short in the existing stage of wear. KU10174, an unworn upper cheek-tooth, has the external groove extending about half way to the base of the tooth, and the hypostria on the internal side extending to a somewhat greater depth, but this tooth has a completely open base, and I suppose crown growth may still take place. It resembles a milk molar in some ways, although wear would produce a pattern like that of $M^1$ or $M^2$ of several species of beavers. A corresponding external fold (mesoflexus) is present in $P^4$ and $M^3$, but is represented by isolated fossettes (mesofossettes) in $M^1$ and $M^2$. An anterior fossette (parafossette) is present in each tooth save $M^3$ where there are two. The corresponding posteroexternal part of each cheek-tooth has two fossettes present, except $M^1$ where only one is present. Of these two fossettes the external one is the metafossette of STIRTON (1935). The second is internal to it, and immediately posterior to the curving end of the mesoflexus. This enamel structure has been termed the submesofossette by CRUSAFONT, VILLALTA, & BATALLER (1948, p. 46). I do not think that at any stage of wear the pattern was complicated as in *Anchitheriomys wiedemanni* and *"Amblycastor" tungurensis.* Some further comment about the subfossette seems justified.

The submesofossette seems usually (or invariably?) to be present in upper cheek-teeth of *Steneofiber castorinus* at a certain stage of wear. It might be assumed that this structure resulted from the isolation of the posterior part of the mesoflexus. This, however, does not seem to be the case. In BM M8155 the cheek-teeth are practically unworn, and it is seen that isolation is the result of an anteriorly placed hypoloph. Hence, the mesoflexus at no time extended to the posteroloph. The additional fossette is, contrary to the name, the result of division of the metafossette by a crest from hypoloph to posteroloph. It would be thought that the similarly placed fossette in *Anchitheriomys?* sp. had a similar origin, but KU10174 indicates that at least in this tooth (deciduous?) the fossette does in fact result from isolation of the mesoflexus. The value to be attached to the manner of development of the submesofossette, and to its presence however brought about, is somewhat uncertain. That it does have some taxonomic importance can be seen by the fact that the submesofossette is present in only one of the many *Monosaulax* specimens from Quarry A, as well as being absent from species of *Monosaulax* and *Dipoides* generally. The chief control of its presence seems, however, to be stratigraphic. The fossette is more generally present in older than in younger species. Therefore it is probably generally present in Oligocene and Aquitanian beavers, and usually absent in post-Aquitanian beavers, if it be permissible to judge on the basis of available specimens and illustrations.

KU10175 is a nearly unworn lower molar, either $M_1$ or $M_2$. Save in size, it agrees almost exactly with an unworn $M_2$ of *Steneofiber castorinus* present in BM 31062. KU10175 also agrees with $M_1$ of a specimen of *S. depereti,* Mus. Lyon, SD 2686 Arbenar, except that in the Lyon specimen the internal grooves are longer. The external groove (hypostriid) extends well down the wall of the tooth nearly to the base, but the tooth is widely open at the base without trace of roots. Roots form early in beavers such as *S. castorinus,* and I suppose in KU10175 they have been broken away. A tendency for delay in the formation of roots in *Anchitheriomys?* sp. may, however, also be involved. Such a tendency possibly is present in *"Amblycastor" tungurensis* for example. Crown height probably is approximately as in *S. castorinus,* but the hypostriid is relatively longer. The mesostriid is a shallow notch in the crown wall. No other striids are present.

The upper incisor is not present. Its alveolus suggests a tooth of trihedral section. The anterior enamel face could have been semiflattened.

*Measurements of* Anchitheriomys? *sp., in Millimeters*

| | KU10173 | KU10175 |
|---|---|---|
| Depth of skull, tip of nasals to lower border of incisors | 33 | ..... |
| Diastema, I-P4 | 39 | ..... |
| Length of nasals | 49 | ..... |
| Interorbital breadth | 17 | ..... |
| $P^4$-$M^3$, ap length (occlusal) | 23.1 | ..... |
| $M_1$-$M_3$, ap length (occlusal) | 15.7 | ..... |
| $M^2$-$M^3$, ap length (occlusal) | 10.5 | ..... |
| $P^4$, ap (occlusal) | 7.5 | ..... |
| tr (occlusal) | 7.7 | ..... |
| $M^1$, ap (occlusal) | 5.5 | ..... |
| tr (occlusal) | 7.0 | ..... |
| $M^2$, ap (occlusal) | 5.5 | ..... |
| tr (occlusal) | 6.8 | ..... |
| $M^3$, ap (occlusal) | 5.0 | ..... |
| tr (occlusal) | 6.0 | ..... |
| $M_1$ or $M_2$, ap (maximum) | ..... | 5.8 |
| tr (maximum) | ..... | 6.1 |

*Relationships.* It seems that *Anchitheriomys?* sp. of Quarry A is more closely related to *Steneofiber castorinus* than to such species of *Palaeocastor* as *P. fossor. P. peninsulatus* and *P. gradatus* of the John Day are closer to the Colorado species in proportions of skull, but it is not clear to me why these should be referred to the same genus as *P. fossor.* Unfortunately, good specimens of certain stratigraphic position have yet to be described for *P. nebrascensis,* the type species of *Palaeocastor.* Assuming, however, that this species is closely related to *P. fossor,* then it seems justifiable to relate the Quarry A species to *Steneofiber* rather than to *Palaeocastor,* as these genera are understood at present. It should be noted that STIRTON (1951, p. 79) thinks that *S. depereti*

had its origin in North America (from *P. peninsulatus* or *P. gradatus*), whereas European authorities such as CRUSAFONT *et al.* (1948, p. 87), think of a European sequence *S. castorinus, S. depereti,* and *S. jaegeri.* This conflict of views suggests why, with the material that I have at hand, it is not possible to say whether *Anchitheriomys?* is more closely related to *Steneofiber,* to the John Day species, or to some other closely allied stock of beavers.

*Anchitheriomys?* sp. is clearly distinct from *Steneofiber castorinus* in larger size, agreeing very nearly in this regard with *S. depereti* of the Burdigalian (and Vindobonian?). But the cheek-teeth of *S. depereti,* are distinctly higher-crowned and have longer grooves. From Vindobonian specimens of *"S. depereti"* (CRUSAFONT *et al.,* 1948), the Quarry A species differs also in the presence of a submesofossette that the former usually lacks.

The robustness of *Anchitheriomys?* sp. suggests a relationship to later forms developing large size. *Monosaulax* is hardly in this category, but *Anchitheriomys* is. An ancestral *"Amblycastor"* could well show the features exhibited by the Quarry A specimen, but lack of material prevents positive support of this theory. In its favor, however, are the following points: (1) *"Amblycastor"* is a large beaver also associated with *Monosaulax;* (2) teeth of *"Amblycastor"* and the Quarry A species seem relatively short-crowned; (3) the mesoflexus tends to be angulate with the external part transverse to the anteroposterior axis of the tooth in both genera; (4) $P^4$ is relatively large in both genera; (5) *Monosaulax senrudi* (H. E. WOOD, 1945) is thought by its author to show resemblances to *"Amblycastor"* to such a degree that at one time WOOD considered referring it to *"Amblycastor"* as a primitive species. *M. senrudi* is comparable in size to the Quarry A species, and the pattern of $M_1$ and $M_2$ probably is like that in the latter when comparable stages of wear are available. This is suggested by observation of the pattern of KU10175 revealed by examination of the open base of the tooth.[17] An additional resemblance between the Quarry A species and *M. senrudi* lies in the relative enlargement of $P\frac{4}{4}$ in respect to $M\frac{1}{1}$. The following measurements illustrate this point.

***Comparison of Ratios in Species of* Monosaulax *and* Anchitheriomys**

| | *Monosaulax,* n.sp. | *M. senrudi* | *Anchitheriomys?* sp. |
|---|---|---|---|
| $LP^4/LM^1$ | 1.13 | ..... | 1.36 |
| $WP^4/WM^1$ | 1.15 | ..... | 1.10 |
| $LP_4/LM_1$ | 1.09 | 1.34 | ..... |
| $WP_4/WM_1$ | 0.91 | 0.94 | ..... |

Possibly *"Amblycastor"* was derived from something like *"Palaeocastor" peninsulatus* by way of *Anchitheriomys?* sp. *Amblycastor,* however, is closely related to *Anchitheriomys* (VIRET in GRASSÉ, 1955, p. 1554; STOUT, 1953, p. 1479; STEHLIN & SCHAUB, 1951, p. 66) of the European Vindobonian (late?) and Sarmatian. Indeed, the two genera are probably synonymous. Possibly the ancestor is to be sought in the Old World, as VIRET (1955, p. 1554) implies, but the ancestor may have been in the New World where possibly the oldest amblycastor is found.[18] Material available to me is not sufficient to answer this question.

The Quarry A species here is tentatively referred to *Anchitheriomys,* although the species probably does not represent that genus strictly speaking. A tentative assignment to *Steneofiber* might be equally as warranted with the present evidence, but conflicting opinion on the scope and phylogeny of the steneofibers make this course perhaps less suitable as a temporary measure. *Anchitheriomys?* sp. is close to *S. depereti* in size, and fairly close in pattern of cheek-tooth. The species from Quarry A seems to be less progressive than *S. depereti,* more progressive than *S. castorinus,* and is distinctly less advanced than *Anchitheriomys.* The morphological evidence suggests a Burdigalian age more than any other.

*Anchitheriomys?* [=Amblycastor?] has been reported from Colorado Miocene deposits before. AMNH9364, an isolated $P^4$ (MATTHEW, 1902, fig. 12; called an upper molar by STIRTON, 1935, p. 413), is reported as coming from near the base of the Pawnee Creek Formation (GALBREATH, 1953, p. 99), and hence may be of like age. That tooth is about the size of KU10174, but the patterns of the two specimens seem to differ.

**MONOSAULAX, n.sp.**

Figures 71-95

*Monosaulax* nr. *M. curtus,* GALBREATH 1953 (p. 98).

Since GALBREATH wrote of this species (1953, p. 98) much additional material has been obtained from Quarry A. Principal additions are: KU9879, a fragmentary mandible with left $P_4$-$M_2$ and right $P_4$-$M_1$, and KU10176, a left maxillary with $P^4$-$M^3$. In addition, there are more than 50 isolated cheek-teeth. In agreement with the stratigraphic position, *Monosaulax,* n.sp., is more primi-

[17] WOOD used *Monosaulax* senrudi to date as "about Barstovian" the beds from which it came. He stated (p. 5), "whether this is really a specialized *Monosaulax,* or a primitive *Amblycastor,* or a borderline species, or a new genus related to both, it would indicate an age that could hardly be far from late Miocene (i.e. Barstovian), and would strongly oppose any assignment to the lower Miocene, whether it be to the Arikaree group proper or to Arikareean time." The presence of the Quarry A species of like size and also showing several resemblances to *"Amblycastor"* suggests some revision of this estimate as well as does the presence of *Monosaulax* at Quarry A. The beds could in fact be upper Rosebud in a restricted sense, and equivalent to the Marsland.

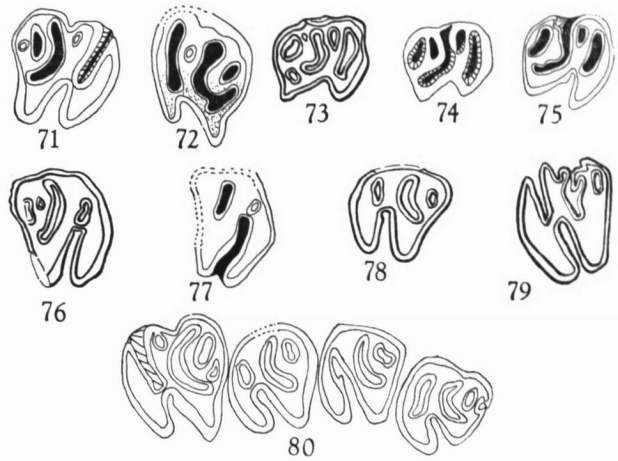
[18] TAKAI (Jap. Journ. Geol. Geog. v. 22, p. 179-180, 1952) indicates *Amblycastor* of Asia *(A. tungurensis?)* as Burdigalian in age, but this seems far too early.

tive than *M. pansus* from Stewart Spring, Nev., a late Hemingfordian locality, or than any other species of the genus, and approaches *Steneofiber* and *Palaeocastor peninsulatus-P. gradatus* more than do other species of *Monosaulax*. In part, this approach may be because of its early stratigraphic position; in part, it may result from special affinities with either or both of these groups. I refrain from naming this species of *Monosaulax* in deference to THOMPSON STOUT's forthcoming work on the Castoridae of the World.

The cheek-teeth of *Monosaulax*, n.sp., seem shorter-crowned than those of the Stewart Spring species which formed the nucleus for STIRTON's (1935, p. 416) description of the genus *Monosaulax*. This is seen in not only actually shorter crowns, but also in the better development of roots, the somewhat shorter hypostriid, and the somewhat more complex crowns of the former (for example, the characteristic presence in moderately worn teeth of a proparafossette—STEHLIN & SCHAUB's synklinale I, 1951). In regard to these characters, the Quarry A species does not appear to be far removed from the stage represented by *Steneofiber castorinus* and is less clearly different from *M. curtus* (MATTHEW & COOK, 1909, p. 381) which is about the same size and was compared by GALBREATH (1953, p. 98) with the Quarry A species. In it the presence of a crescentic parafossettid which GALBREATH *(loc. cit.)* mentions is not altogether constant, and may well be present in some individuals of *M. curtus*. STIRTON (1935, p. 420) says of *M. curtus* that it is to be distinguished from *M. pansus* only by lesser size, and if this be so, then *M. curtus* is distinct from *Monosaulax*, n.sp., in the features already cited as distinguishing *M. pansus*. In any case, *M. curtus* is from a later horizon.

From typical *Palaeocastor*, the Quarry A species is to be distinguished especially by the cross-sectional shape of the incisors—rounded rather than flat. From *Steneofiber castorinus*, the Quarry A species differs as follows: (1) in $P^4$, the paraflexus persists longer than the mesoflexus, a special characteristic of the *Monosaulax-Dipoides* line; (2) the anterior lobe of $P_4$ is more angulate, and less rounded, the parafossettid, although complex in unworn condition, not existing as a flexid anteriorly as in *Steneofiber* (*S. castorinus, S. jaegeri, S. depereti* all agree in this); (3) in the lower molars, the protoconid pillars are more acute, the proparafossettid less well developed, and the mesoflexid slightly more persistent than in *S. castorinus* where it is characteristically never seen; and (4) the origin of the ascending ramus of the mandible is more posterior in the American species being (in 9879) approximately opposite $M_2$ rather than opposite $M_1$ as in *S. castorinus*.

Features (1), (2), and (3) are in general characteristic of the *Monosaulax-Dipoides* line, and with the shape of the lower incisor prevent assignment of the Quarry A species to any genus other than *Monosaulax*. Nevertheless, there is a decided similarity between *Monosaulax*, n.sp., and *S. castorinus* in many features. For example, rather faint furrows, somewhat diverging, are present on the lower incisors of both species; $Dp_4$ is similar in each possessing only one striid to the inside (a point of distinction from *M. minutus* which has two internal striids); the basic molar patterns are close.




FIGURES 71-80. *Monosaulax*, n. sp.————71, Right $P^4$, KU10177a.————72, Left $P^4$, KU10177b.————73, Right $M^1$ or $M^2$, KU10181.————74, Right $M^1$, KU10178a.————75, Right $M^1$, KU10178b.————76, Right $M^1$, KU10178c.————77, Right $M^1$, KU10178d.————78, Left $M^2$, KU10179.————79, Left $D^m$, KU10182.————80, Left $P^4$-$M^3$, KU10176. [All ×4.5 except Fig. 80, ×4.]

The principal features in *Monosaulax*, n.sp., of the individual teeth may be summarized as follows:

(1) $P^4$: Hypostria extending to somewhat past mid-point of crown wall; paraflexus much shorter, but persistent for some distance; other two folds (mesoflexus, metaflexus) early converted to fossettes; secondary small fossettes sometimes present, one posterior to the parafossette (subparafossette), and other posterior to metafossette (submetafossette).

(2) $M^1$-$M^2$: These teeth cannot be certainly told apart when occurring as isolated finds. Hypostria, in most cases, extending nearly to base of tooth; short mesostria present in unworn or little worn teeth, but para- and metafossettes already present in nearly unworn teeth; subparafossette and prometafossettes may be present briefly.

(3) $M^3$: Hypostria nearly to base; parafossette always present; mesoflexus present in unworn specimens with shallow notch at external border; metaflexus tending to open posteriorly through shallow notch even after some wear; subparafossette can be present.

(4) $D^m$: In available stage of wear, paraflexus, mesoflexus (complex), and hypoflexus present; metaflexus reduced to a fossette.

(5) $\underline{I}$: Rounded anterior face; enamel with faint slightly divergent furrows.

(6) $P_4$: Anterior lobe angulate, and smaller than posterior one; hypostriid extending nearly to base of tooth in unworn state; parafossettid usually crescentic, but variable in pattern and shape, always present as a fossettid (except in a single specimen where continuous with mesoflexid), sometimes with a proparafossettid;

mesoflexid short, but present in early stages of wear; metafossettid always present as a fossettid.

(7) $M_1$: Protoconid and hypoconid pillars angulate; hypostriid extending halfway to base of tooth, or perhaps somewhat longer in some; proparafossettid present in early stage of wear; parafossettid usually more or less crescentic in shape, always present as a fossettid; mesostriid present, but short; metaflexid as a notch in wall of tooth in earliest stage of wear.

(8) $M_2$: Resembling $M_1$, but shorter crowned; hypostriid probably slightly shorter on average.

(9) $M_3$: Rounded posterior margin; hypostriid extending from halfway nearly to base of tooth; proparafossettid present in early stages of wear; parafossettid usually (always?) present; mesostriid short; metaflexid tending to be continuous with hypoflexid in early stages of wear.

(10) $D_m$: Parafossettid and metafossettid always present; mesoflexid present with extremely short mesostriid.

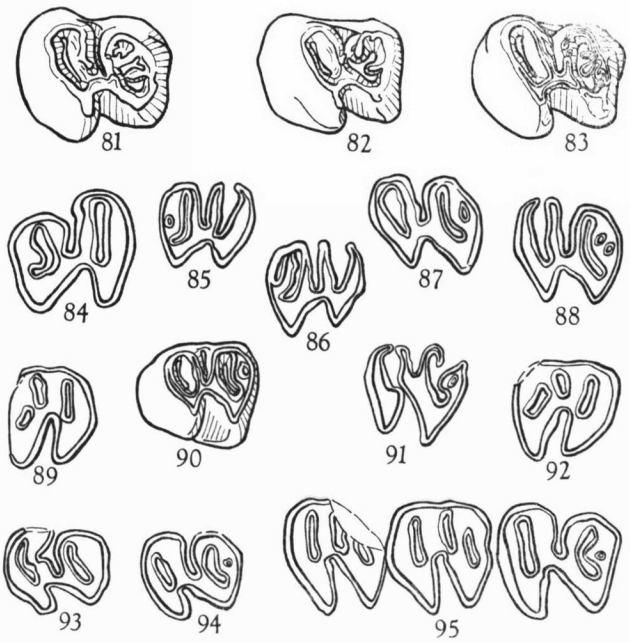
*Measurements of Species of* Monosaulax, *in Millimeters*

| | *M.*, n.sp. | *M. curtus* | *M. minutus*(a) |
|---|---|---|---|
| $P^4$-$M^3$, ap occlusal | 11.8 | ..... | ..... |
| $P^4$, ap occlusal | 3.3 | ..... | ..... |
| tr occlusal | 3.8 | ..... | ..... |
| $M^1$, ap occlusal | 2.9 | ..... | ..... |
| tr occlusal | 3.3 | ..... | ..... |
| $M^2$, ap occlusal | 2.6 | ..... | ..... |
| tr occlusal | 3.3 | ..... | ..... |
| $M^3$, ap occlusal | 2.8 | ..... | ..... |
| tr occlusal | 3.0 | ..... | ..... |
| $P^4$, ap | 3.8-3.9 | ..... | 4.1-4.8 |
| tr | 4.1-4.4 | ..... | 4.1-4.7 |
| $M^1$ and $M^2$, ap | 2.6-3.1(2.8+) | ..... | 2.55-3.1 |
| tr | 3.2-4.0-(3.5+) | ..... | 3.55-4.1 |
| $M^3$, ap | 3.0-3.2 | ..... | 3.7-4.1 |
| tr | 3.0+-3.5 | ..... | 2.8-3.6 |
| $D^m$, ap | 2.8 | ..... | ..... |
| tr | 3.8 | ..... | ..... |
| $P_4$-$M_2$, ap occlusal | 9.7-10.4 | 9.9 | ..... |
| Diastema, $\bar{I}$-$P_4$ | 11.0 | ..... | ..... |
| $\bar{I}$, tr | 3.5 | 3.0 | 2.5-2.8 |
| $P_4$, ap occlusal | 3.5, 3.9 | ..... | ..... |
| tr occlusal | 3.2, 3.7 | ..... | ..... |
| $M_1$, ap occlusal | 3.2, 3.4 | ..... | ..... |
| tr occlusal | 3.5 | ..... | ..... |
| $M_2$, ap occlusal | 3.0 | ..... | ..... |
| tr occlusal | 3.7 | ..... | 3.86 |
| $P_4$, ap | 4.6-5.2(4.9) | ..... | 5.57 |
| tr | 3.9-4.2(4.0) | ..... | 4.38 |
| $M_1$, ap | 2.8-3.4(3.0) | ..... | 3.12 |
| tr | 3.3-3.8(3.5) | ..... | 3.92 |
| $M_2$, ap | 2.8-3.2(3.0) | ..... | 2.9 |
| tr | 3.1-3.6(3.4) | ..... | 3.86 |
| $M_3$, ap | 3.0-3.2(3.0) | ..... | 2.8 |
| tr | 3.0+-3.4(3.2+) | ..... | 3.6 |
| $D_m$, ap | 3.2, 3.5 | ..... | 3.6 |
| tr | 2.8, 3.0 | ..... | 3.18 |

(a) *Monosaulax minutus* from Vindobonian of Spain; measurements of these taken at base of tooth (wear, stage 5 of CRUSAFONT *et al.*).

### REMARKS ON FOSSIL CASTORIDS

*Monosaulax* as now known in North America ranges from the Marsland (and equivalents) to the close of the Miocene (as defined by the end of the Barstovian). Presumably *Monosaulax* is transformed at about this time into *Eucastor* of the early Pliocene. At the older end of its range, it shows increasing resemblance to *Steneofiber castorinus* and other beavers in a comparable stage of evolution. Presumably the ancestors of *Monosaulax,* n.sp., are known but have not been recognized as such. Judging from the stage of development of the Quarry A specimens, discrimination of the line in pre-Marslandian time should be possible, if it is continued in America, and is not an immigrant species.




FIGURES 81-95. *Monosaulax,* n. sp.————81, Right $P_4$, KU10185a.————82, Right $P_4$, KU10185b.————83, Right $P_4$, KU10185c.————84, Left $P_4$, KU10186.————85, Right $M_1$, KU10190a.————86, Left $M_1$, KU10190b.————87, Right $M_1$, KU10190c.————88, Left $M_2$, KU10191a.————89, Left $M_2$, KU10191b.————90, Right $M_3$, KU10192a.————91, Right $M_3$, KU10192b.————92, Left $M_3$, KU10192c.————93, Right $D_m$, KU10187a.————94, Right $D_m$, KU10187b.————95, Right $P_4$-$M_2$, KU9283. [Figs. 81-84, ×4; Figs. 85-88, 92-95, ×4.5; Figs. 89-91, ×4.25.]

STIRTON (1935, p. 423-425) tentatively recognized the genus *Monosaulax* in Europe, and assigned *Chalicomys minutus* and *C. eseri* to the genus. Subsequently CRUSAFONT *et al.* (1948, p. 69-81) somewhat more positively listed its presence, but assigned only *C. minutus* to it. I have not seen sufficient material to form a firm opinion regarding the generic position of *C. minutus,* but that it is a species of *Monosaulax* certainly cannot be

rejected offhand. *"M." minutus* of the Sansan agrees with *Monosaulax,* n.sp., in size, but the latter seems more primitive, as for example in retention for a longer time of some small enamel fossettes. Although individual teeth could be matched in the two species, the shape of the anterior lobe of $P_4$ is different, and more reminiscent of that of *Steneofiber.*

STIRTON (1935, p. 450) suggested tentatively that *"Monosaulax" eseri* or *"M." minutus* might have given rise to *Trogontherium.* In this regard, the specimens of *"M." minutus* figured by STROMER (1928) from the Flinz are instructive in their enlarged third upper molars, which are suggestive of those of *Trogontherium.*

CRUSAFONT *et al.* (1948, p. 69-81) regarded *Chalicomys eseri* as a synonym of *Steneofiber castorinus,* which has usually been the opinion of European workers. STIRTON (1935, p. 424, fig. 82) lists and figures the type of *C. eseri* as a left lower jaw with incisor and $P_4$-$M_3$(although calling attention to VON MEYER's reference to it as a right lower jaw) from "Oeninger mergels im Oerlinger Thal bei Ulm Württemberg." The figure by STIRTON certainly is not of the type. It is a copy of one by SCHLOSSER (1885, pl. VI, fig. 3), and the latter author states it is from Haslach bei Ulm in the legend of plate VI, but as from Eggingen bei Ulm in the text (p. 22). Figures of the actual type seem to have been overlooked. First use of the name *Chalicomys eseri* was by VON MEYER in the *Neues Jahrbuch* for 1846, as cited by STIRTON. But there it is a *nomen nudum.* Later in the same year (after July, according to SHERBORN, p. 1132), a description of *C. eseri* was published together with a figure of a right lower jaw from Oerlinger Thal bei Ulm, evidently the type, although the text does not make this clear to me (*Jahresheften Ver. Vaterländische Naturk. Württemberg,* ser. 2, v. 2, p. 147, pl. 3, figs. 1a,b). This second description is listed by SHERBORN as validating the name *C. eseri* and evidently has priority over *S. castorinus* POMEL (1847?) if only a single species in involved; the reference in CRUSAFONT *et al.* (1948, p. 47) to VON MEYER's use of *Steneofiber eseri* in 1838, which would presumably make *C. eseri* the type of *Steneofiber,* I am unable to find in the work cited. The Oeninger marls are late Miocene in age, but as I read the original, VON MEYER says only that the specimen came from beds like the massive marls of Oeninger.[19] At any rate, the Haslach and Eggingen faunas, with which STIRTON's specimen is to be associated, are Aquitanian, not Vindobonian. British Museum 35747-8 are specimens from Haslach with label *Steneofiber eseri.* They represent a relatively large mandible, $P^4$, and incisor, but otherwise than in their atypical size agree with specimens of *S. castorinus* from Allier. In several features of the cheek-teeth they differ from those of *Monosaulax.* Judging also from the figure of the type, *C. eseri* belongs in the genus *Steneofiber,* rather than *Monosaulax,* although this specimen has a well-worn dentition in which flexids are transformed into fossettids. In size, the type corresponds to that of *S. castorinus,* or, more exactly, the side view of the ramus is the size of BM35747, from Haslach; the occlusal view of the cheek-teeth, is of the same size as various specimens of *S. castorinus* from Allier. Resemblance to *Steneofiber* is seen in: (1) roundness of the protoconid-hypoconid pillars; and (2) the general shape of $P_4$, as well as in the anterior exit of the parafossettid suggested by the drawing. I have not been able to ascertain what section is exposed at Örlinger Thal, but I assume that the resemblance to beds at Öninger would not prohibit assignment to the lower Süsswasser molasse, rather than to the upper.

*Steneofiber castorinus* and *S. eseri* are probably synonyms as most have thought, but on the basis of material so far available to me I can not be sure of it. Consequently, I am continuing to use the name *S. castorinus* for the Aquitanian specimens from France. I assume that *Steneofiber* GEOFROY is a valid and available name for this genus of beavers, although I have not consulted the original source (*Consid. Oss. foss. Auvergne,* 1834) cited by SHERBORN (p. 6138) and by NEAVE (v. 4, p. 286) as the type description.[20]

Almost all have assumed that *Chalicomys* and *Palaeomys* are synonyms. STIRTON (1935, p. 425) cites the type species of the former as from Mainz and that of the latter as from Weisenau. This stand, originally made in 1935, he repeats in 1951 (1948, *Int. Geol. Congress,* p. 77), as follows: "I am convinced that KAUP's original type of *Palaeomys castoroides* did come from beds of Aquitanian age, possibly Weisenau; though I now feel that *P. castoroides* is not synonymous with his *Chalicomys jaegeri* from Eppelsheim." KAUP's type description (1832, p. 991; and KAUP, 1833, p. xv) has them both coming seemingly from Eppelsheim, not merely from the Eppelsheim fauna. Further, the Weisenau fauna, as such, is Aquitanian. The Eppelsheim fauna, on the other hand, is Pliocene and post-Sarmatian.

If *Steneofiber jaegeri,* the type of *Chalicomys,* is from the Eppelsheim fauna, there seems to be small probability that it is congeneric with the Aquitanian *S. castorinus* or that it is specifically identical with Vindobonian species, as is usually said to be the case, if evolutionary

[19] "Im Örlinger Thal bei Ulm kommt ein den nicht schiefrigen Lagen des Öninger Mergels sehr ähnliches Süsswasser Gebilde vor, woraus Hr. Finanzrath Eser mir die rechte Unterkiefer-Hälfte mit der vollstandigen Backenzahn-Reihe von einem Nager mittheilte, der einer neuen Spezies von *Chalicomys, Ch. Eseri,* angehört," (VON MEYER, 1846, p. 474).

[20] Usually cited is *Revue Encyclopedique,* 1833. This does contain the first description of the genus, but under the name *Steneotherium.* According to SHERBORN, *Steneofiber* (1834) is a substitute name for it, but on what grounds the name was replaced I do not know.

sequences of beavers from North America are any guides. One might infer from the lack of reference to *Anchitheriomys* by CRUSAFONT *et al.* that these authors regard *A. weidemanni* and *S. jaegeri* as synonyms, but this synonymy seems highly unlikely, although some specimens referred to *S. jaegeri* might be of the genus *Anchitheriomys*. Thus, it may be that the large beaver from the Vindobonian and Sarmatian usually called *S. jaegeri* should be called *S. subpyraenicus*. STEHLIN, however, has opposed this point of view (STEHLIN & HELBING, 1925, p. 25-27). Certainly on no evidence that I know can the name combination *Steneofiber jaegeri* (KAUP) be justified, in as much as *Chalicomys* is an older generic name. Some similarity between *"S." jaegeri* and *Hystricops venustus* of the New World may be noted, but material of the latter has always been most scant.

All in all, a revision of the European, as well as the American, beavers is much needed, and it is hoped that STOUT's work on the Castoridae, shortly to be published, will provde us with a stable and satisfactory nomenclature. The importance of the shape of the incisors, particularly, needs careful reconsideration. STIRTON (1935) has stressed this shape to separate lines of beavers that usually have not been distinguished. It is an obvious enough character; for example, it separates *Dipoides* from *Castor* and *Palaeocastor* from *Stenofiber*, but these lines are separable on other bases. Where the incisors are neither sharply rounded nor flat, or where their shape is in disagreement with characters exhibited in the cheek-teeth, then what is the proper procedure? Classification on incisor shape possibly has led STIRTON (1935) to incorrect assignments in several cases (e.g., *"Monosaulax" complexus, "M." hesperus*).

## Suborder MYOMORPHA

In addition to the Dipodoidea traditionally referred to the suborder Myomorpha, I have placed here also the Geomyoidea (including the Eomyidae). This treatment agrees with that of WOOD (1955) and formally carries out an earlier suggestion of mine (WILSON, 1949). Beyond what I then stated (1949b, p. 42-48, 155), I may note that: (1) in the Geomyoidea, according to J. E. HILL (1937, p. 157), the reproductive organs are highly suggestive of the muroids and, principally on this basis, HILL (op.cit., p. 161) transferred the Geomyidae to the Myomorpha; and (2) in the summer of 1956 a field party of the Museum of Natural History, University of Kansas, was fortunate in finding part of the skull of *Heliscomys* showing the basicranial region, which specimen is now being studied by Dr. E. C. GALBREATH, who reports that the basicranial region closely resembles that of some cricetids.

An interesting, if negative, aspect of the Quarry A fauna is the absence of all representatives of the Muroidea. Heteromyids and zapodids seem to have been mostly in their places in North America for much of the Miocene.

### Superfamily GEOMYOIDEA

### Family EOMYIDAE

Post-Oligocene occurrences of the family Eomyidae are rare in North America. Indeed, this is the first such record, unless *Kansasimys* (Ogallala, Pliocene) is also one. It is even more unexpected that the new record pertains to *Pseudotheridomys*, a European genus, rather than to the American eomyid group typified by *Adjidaumo* and *Paradjidaumo*. The American *Pseudotheridomys* seems to have been an element in the general faunal interchange between Eurasia and North America at the beginning of Burdigalian time. Interesting in this regard is the fact that the species is less progressive than *P. carpathicus* of the early Vindobonian of Europe.

#### PSEUDOTHERIDOMYS HESPERUS Wilson, n.sp.

Figures 91-101

*Holotype.* Incomplete right lower jaw having incisor and $P_4$-$M_2$, No. 10195, Univ. Kansas Mus. Nat. Hist.

*Referred specimens.* KU10196-KU10198, fragmentary lower jaws; KU10199, left $P_4$; KU10200, fragment of right maxillary having $P^4$; KU10201, right $M^2$; and ?KU10202, right $M^1$.

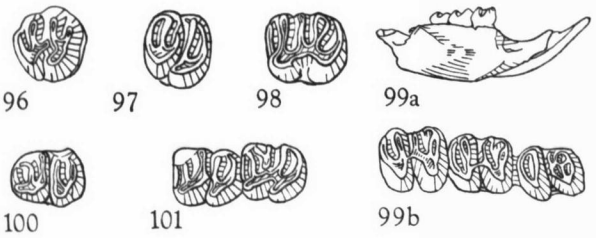
*Geological age and locality.* Sandy silts of Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Diagnosis.* Size of *Pseudotheridomys parvulus*, larger than *P. carpathicus*. Anterior valley (*aussensynklinale* I) of upper molars closed and relatively long, union of paracone to protocone central rather than anterior in respect to latter, endoloph (mure) probably slightly less continuous than in *P. parvulus*, and more so than in *P. carpathicus*, internal embayment between protocone and hypocone not extended internally as in *P. carpathicus*. $P_4$ having anterointernal exit of anterior valley (*innersynklinale* I). Ectolophid less continuous than in *P. carpathicus*. Metastylids present. Lower molars more elongate than in *P. parvulus* or *P. schaubi*.

*Description and comparisons.* The upper dentition is known by $P^4$ and $M^2$, and probably by a first molar as well.

The fourth upper premolar has a fundamental pattern quite like that in the European species of *Pseudotheridomys*. [For this genus see STEHLIN & SCHAUB, 1951; SCHAUB, 1953; and especially SCHAUB & ZAPFE, 1953.] Several points deserving special mention are: (1) the

anterior valley is present and open (though usually absent in *P. carpathicus*); (2) the most posterior valley is likewise open, but only slightly; (3) the mesoloph is rudimentary. In *P. parvulus* the mesoloph reaches the internal border of the tooth in some specimens, and the mure (endoloph) is not connected to the trigon. The mure is connected in *P. parvulus,* and the embayment between protocone and hypocone is of moderate depth.




FIGURES 96-101. *Pseudotheridomys hesperus.*————96, Right $P^4$, KU10200.————97, Right $M^2$, KU10201.————98, Right $M^1$, KU10202.————99, Type specimen, right lower jaw with $P_4$-$M_2$, KU10195; 99a, lateral view; 99b, occlusal view of cheek dentition.————100, Left $P_4$, KU10197.————101, Occlusal view of left $M_1$-$M_2$, KU10196. [All ×10, except 99a, ×3.3.]

KU10202 probably is an $M^1$ of *Pseudotheridomys hesperus,* but may be an upper molar of a zapodid. It is much like the $M^1$ in *P. parvulus* having a cricetodontid pattern of five crests separated by four intervening valleys. The most outstanding difference lies in the structure of the most posterior valley, which is open to the inside. That valley has not been described as occurring in *P. parvulus* although the anterior valley in the lower molars may cut through to the outside (thus a mirror image). Also the long anterior valley seems to be more nearly closed than in *P. parvulus*. The mesoloph is long, extending to the outer border of the tooth. $M^1$ is notably unlike that tooth in *P. carpathicus* differing especially in the length of the anterior valley and the shallowness of the internal embayment between protocone and hypocone with consequent lack of restriction of the next valley posterior.

The second upper molar, KU10201, is certainly referable to *Pseudotheridomys hesperus*. In its critical features it is more nearly like that of *P. parvulus* than that of *P. carpathicus*. Thus, the embayment between protocone and hypocone is relatively shallow, the anterior valley relatively long, and the point of attachment of the paracone crest to the protocone is central rather than anterior. These are all features stressed by SCHAUB & ZAPFE (1953, p. 183-189) as important in distinguishing *P. parvulus* from *P. carpathicus*. On the other hand, the endoloph (mure) is disjunct and these authors suggest that this structure *(langsgrat)* is complete in *P. parvulus*. Nevertheless, this seemingly is not always true of $M^2$ (SCHAUB, 1953, p. 22, fig. 39). The anterior valley is also closed, and in this feature the American species resembles *P. carpathicus,* although seemingly the valley is occasionally closed in *P. parvulus*. The mesoloph, although well developed, does not reach the external border of the tooth.

The lower jaw shows some points of dissimilarity from that of *Pseudotheridomys carpathicus* as figured by SCHAUB & ZAPFE (1953, fig. 1). For one thing, the diastema is relatively longer with alveolar sheath more procumbent. The tip of the incisor is below rather than above the level of the occlusal surface of the cheek-teeth, and this, I suppose, is not the result of slipping of the incisor forward in its alveolus. In length of diastema the jaw agrees fairly well with that of *P. parvulus* as measured by SCHLOSSER (1884, p. 62). The masseteric scar in *P. hesperus* seems more acutely pointed anteriorly than that figured by SCHAUB & ZAPFE. Nevertheless, actual comparison of specimens of *P. hesperus* and *P. parvulus* reveals no outstanding differences insofar as comparisons can be made. The mental foramen, considerably in advance of the cheek-teeth, is conspicuous on the alveolar collar of the incisor. A dental foramen is present at the anteroinferior margin of the pterygoid fossa.

The incisor of *Pseudotheridomys carpathicus* is described (SCHAUB & ZAPFE, 1953, p. 188) as rather strongly compressed and narrowly elliptical in cross-section. This description may be applied to ours as well.

The lower teeth, and the uppers, are modifications in pattern of a cricetodontid type. The fourth lower premolar is known by three specimens, KU10195, KU10197, and KU10199. They show the ectolophid to be cut through in this tooth (although possibly uniting with wear), as in *Pseudotheridomys parvulus* but not in *P. carpathicus*. Unlike the upper teeth, $P_4$ has the mesolophid joined to the front part of the tooth (trigonid) and free of the hinder (talonid). The mesolophid is moderately long but joined with the metaconid with the result of closing the valley immediately in front. This feature is present in *P. carpathicus* and probably also in *P. parvulus* on occasion, although SCHAUB & ZAPFE (*op. cit.,* p. 187) state that the second valley in the latter is open. The most anterior valley opens anterointernally through a slight notch. SCHLOSSER (1884, pl. 3, fig. 26) figures a similar condition in *P. parvulus* and I have seen actual specimens which also show this. The postentoconid valley is closed or nearly so in all three specimens. A metastylid can be made out in two of the specimens (the third is broken, and its presence uncertain).

The first lower molar is also known in three specimens of *Pseudotheridomys hesperus,* but in one (KU10196) this tooth is broken, and in another (KU10198) too worn for use. The ectolophid is continuous, but barely so in the available specimens. The mesolophid is long and reaches the inner margin of the tooth; perhaps this crest is longer than in *P. carpathicus*. The post-

entoconid valley is questionably described as open. The valley immediately in advance of the mesolophid (*innersynklinale* II) is open. The most anterior valley is present in KU10195 as a barely discernable remnant but in 10196 is present as a long, narrow valley that breaks through slightly on the external side in the manner shown by $M_1$ of *P. parvulus* in a specimen from Weisenau (STEHLIN & SCHAUB, op. cit., p. 293, fig. 508).

The second lower molar is represented in KU10195 and KU10196, but the pattern is somewhat clearer in KU10196 than in the type. The ectolophid is connected, but weakly, in KU10196, and seems disjunct, although barely so, in KU10195. The mesolophid extends to the inner side in both, joining the metaconid in KU10196, but not in 10195. Thus the valley immediately anterior to the mesolophid is closed in the former and open in the latter. The most anterior valley (*innersynklinale* I) is essentially shut in KU10196 and small but shut in KU10195. A metastylid cuspule is present in KU10196, but seems to be absent in KU10195. A somewhat similar structure (metastylid?) seems to be present in the molars of *P. schaubi* (LAVOCAT, 1951, pl. 5, fig. 8). The postentoconid valley is closed. If all available figures and specimens of *P. parvulus* are used, there seems to be no essential difference between it and *P. hesperus*. In comparison with *P. carpathicus,* the most obvious distinction is in the shortening of mesolophid of the specimen figured by SCHAUB & ZAPFE (*op. cit.,* pl. 1, fig. 7), but this shortness seems subject to individual variation.

*Measurements of* Pseudotheridomys, *in Millimeters*

| | *P. hesperus* | *P. parvulus*(a) | *P. carpathicus*(b) |
|---|---|---|---|
| Length of diastema, $\bar{I}$-$P_4$ | 2.4?-2.7 | 3.0 | ..... |
| Alveolar length, $P_4$-$M_3$ | 3.7 | 3.8-4.2 | 2.60-2.75 |
| $P_4$-$M_2$, ap | 2.9 | ..... | ..... |
| Depth of jaw beneath $M_2$ | 1.8-2.2+ | ..... | ..... |
| $\bar{I}$, tr | 0.6 | ..... | ..... |
| $P_4$, ap | 0.9-1.0 | 1.0 | 0.59-0.71 |
| tr | 0.7-0.9 | 0.9 | 0.61-0.69 |
| $M_1$, ap | 1.0-1.1 | 1.2 | 0.71-0.82 |
| tr | 1.0-1.1— | 1.1 | 0.71-0.82 |
| $M_2$, ap | 0.9-1.0— | 1.1 | 0.64-0.71 |
| tr | 1.0— | 1.1 | 0.66-0.77 |
| $P^4$, ap | 1.0 | 0.9 | 0.56-0.66 |
| tr | 1.0 | 1.0 | 0.64-0.71 |
| $M^1$, ap | 1.2— | 1.0 | 0.69-0.77 |
| tr | 1.1 | 1.0 | 0.71-0.82 |
| $M^2$, ap | 1.0 | 0.9 | 0.56-0.69 |
| tr | 1.1 | 1.0+ | 0.71-0.82 |

(a) Chiefly composite of measurements taken from various illustrations and not to be used for more than a rough indication of size.

(b) From SCHAUB & ZAPFE (1953).

Of the two previously recognized species of post-Stampian age, *Pseudotheridomys parvulus* and *P. carpathicus,* the former is close in all characteristics including size to the Colorado species. Considerable individual variation is present in the dentition of *Pseudotheridomys* (STEHLIN & SCHAUB, 1951; SCHAUB, 1953, p. 22; SCHAUB & ZAPFE, 1953). With the small sample available from Quarry A, it becomes difficult, in view of the known variation in named species, to arrive at a clean cut, complete separation of specimens of *P. parvulus* from those of *P. hesperus*. In general, however, *P. hesperus* is to be distinguished by: (1) more elongate (narrower) lower molars; (2) closure of anterior valley in upper molars; (3) greater tendency for a disjunct mure (endoloph) in the upper dentition; (4) presence of metastylids; and (5) possibly a slightly greater tendency for breakthrough of the ectolophid in lower molars, SCHLOSSER's figures (1884, pl. 3, fig. 26), however, showing a pronounced breakthrough, as well as do specimens examined by me. The distinctions from *P. carpathicus* are much more obvious, including a larger size. The principal ones have been mentioned earlier, and will not be repeated here. In the presence of metastylids, and possibly in the somewhat greater tendency for discontinuous ectolophid-mure structures, *P. hesperus* seems to be advanced over *P. parvulus*. It seems distinctly less specialized than *P. carpathicus*. On the whole, I have received the impression that additional specimens of more complete nature would strengthen the distinctness of *P. hesperus* rather than lessen it. There is no reason, however, to think that *P. hesperus* pertains to a closely related genus rather than to *Pseudotheridomys* itself.

It is tempting to make use of *Pseudotheridomys* for correlation between Europe and North America. This genus is an eomyid, and eomyids are known from the Oligocene of both continents. However, it is unlike any North American eomyid of the Oligocene. The genus appears for the first time in the Stampian with the species *P. schaubi*. *P. parvulus* is younger, having a known range of Chattian to the late Aquitanian and probably early Burdigalian. *P. carpathicus* of the early Vindobonian (Helvetian) marks the last known appearance of the genus in Europe. Although possibly *P. carpathicus* is a descendant of *P. parvulus,* this can not be established at present. *P. hesperus* almost certainly represents an Old-World migrant, and could well have descended from *P. parvulus*. Since it is not so specialized as *P. carpathicus,* the known facts, admittedly extremely difficult to evaluate, suggest a Burdigalian age for *P. hesperus*. The Quarry A species is possibly more advanced than European species from the lower Burdigalian, but essentially *P. parvulus* and *P. hesperus* are at the same evolutionary stage. In this connection, it may be noted that STIRTON (1951, p. 78) comments on the intercontinental dispersals which took place at the beginning of the Burdigalian, a time which he correlates (p. 79) with the beginning of Marslandian deposition.

The Stampian *Pseudotheridomys schaubi* seemingly agrees with *P. hesperus* in the possession of metastylids,

but the cheek-teeth are less elongate. Relationship of *P. schaubi* to *P. hesperus* seems less close than between the latter and *P. parvulus.*

DEHM (1950, p. 407-413) has described as *Eomys lophidens* a Burdigalian eomyid from Winterhof-West bei Eichstatt. I first judged from his figures that *E. lophidens* was not properly referable to *Eomys,* but to some other genus. The lower molars lack the characteristic attachment of the entoconid to posterolophid of *Eomys. E. lophidens* seemed to show a much greater resemblance to *Pseudotheridomys.* I suspected, however, that its relationships were really with *Ligerimys.* Later, Dr. S. SCHAUB informed me that *E. lophidens* was in fact a composite of *Ligerimys* and *Pseudotheridomys (P. parvulus?).* The type pertains to *Pseudotheridomys.*

The presence of *Pseudotheridomys* in North America calls for a partial, and in reality inconsequential, correction of SCHAUB's statement that in North America "the Theridomys-plan is completely absent and there is not even the slightest trace of forms which, in respect to their tooth-pattern, could be ancestral to this plan" (SCHAUB, 1953a, p. 392). *Pseudotheridomys* of Europe, to quote further (p. 393), "have . . . like the true *Theridomys,* the tendency to transform their molar structure into the Theridomys-pattern, but this is realized only in a few cases." Now there is some evidence for the presence of rodents in North America that could transform their molar patterns into a theridomyidlike one. SCHAUB (1953a, p. 391-393) holds that this theridomyidlike plan is basic for the South American hystricomorphs. Obviously, *P. hesperus* is much too late in time to be a prospective "hystricomorph" ancestor, and I do not think it has a North American ancestry. Also, if an eomyid as believed, it is completely unlike the hystricomorph group in zygomasseteric structure. We have, then, no additional evidence on the hystricomorph problem, unless the presence of a species with a tooth pattern potentially theridomyidlike is to be regarded as an item for remembrance.

## Family HETEROMYIDAE

Heteromyid specimens are reasonably common in the Quarry A assemblage, but consist almost entirely of isolated teeth. Only in four specimens are two or more cheek-teeth in association. At least two species are present. One, a rare, relatively giant species, is represented only by a few scattered teeth. It appears to be related to *Proheteromys magnus.* The remainder of the specimens form a heterogeneous assemblage highly variable both as to size and structure of teeth. It at first seemed that almost surely two species of two different genera were present. But, careful study of the whole failed to reveal any clear-cut separation, and possibly only a single highly variable species is present. I have compromised to the extent of separating a few fragmentary specimens from the main lot for separate recognition. Whatever the true taxonomic relations, the variability expressed by this collection is sufficient to include several of the described heteromyids of equivalent age (*Mookomys formicorum, Proheteromys matthewi,* and *P. floridanus*—save in slightly different size). Regardless of how many species are represented, all the specimens are of the same general evolutionary level, and probably give a fair idea of what is otherwise a rather poorly known stage of normal heteromyid evolution in the Plains area. It seems that at this Miocene level the distinction between perognathine and heteromyine, for example, is difficult to make, and that the molars resemble those of the Oligocene *Heliscomys,* especially in the weak development of the hypostylid and posterior position of the protostylid in the lower molars.

### PROHETEROMYS SULCULUS Wilson, n.sp.

Figures 102-114

*Proheteromys* spp. *(partim),* GALBREATH, 1953 (p. 97).

*Holotype.* Left lower jaw bearing $P_4$-$M_2$, No. 10203, Univ. Kansas Mus. Nat. Hist.

*Referred specimens.* Skull fragment bearing incisors and right $P^4$, KU10204. Right maxillary fragment bearing $M^1$-$M^2$, KU10205. Various upper cheek-teeth, KU-10206-KU10216. Fragment of left lower jaw bearing $P_4$-$M_2$, KU10217. Various lower cheek-teeth, KU10218-KU10230.

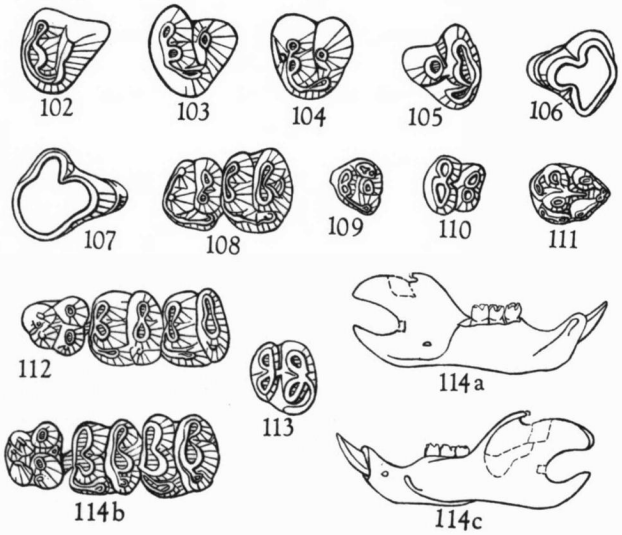
*Geological age and locality.* Sandy silts of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE ¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Diagnosis.* Size approximately that of *Proheteromys matthewi, P. thorpei,* or *Mookomys formicorum.* Upper incisor weakly sulcate. Incipient J-pattern in $P^4$, lacking accessory cuspules in protoloph. $M^3$ having cusps surrounding a central basin. Anterior end of masseteric crest relatively distinct. Lower incisor somewhat flattened on anterior surface. $P_4$ having stylids usually present, mesoconid well-developed, and principal external cusps closer together than those of internal pair. Lower molars having weak hypostylids, altogether absent on $M_3$. $M_1$ usually, $M_2$ less frequently, having H-pattern.

*Description.* The skull fragment, KU10204, is too incomplete to contribute much to our knowledge of osteology of early Miocene heteromyids except that it provides a certain association between upper incisors and one kind of $P^4$ pattern. Other specimens contribute somewhat more information concerning the palate, and seem to show that it was slightly ridged between the premolars, or perhaps slightly ridged in some and completely smooth in others.

The upper incisors are broadly and shallowly grooved. A somewhat similar type of grooving is seemingly described by A. E. WOOD (1935, p. 179) in the "Pliocene" species, *Diprionomys agrarius.*

The cheek-teeth exhibit slightly lengthened crowns, but the individual cusps are usually distinct even after considerable wear. In the upper dentition, $P^4$ is perhaps slightly the widest tooth in the cheek series. No direct association, however, of this tooth with any other cheek-tooth is known, and this statement is based on measurements of teeth not of the same individual. The molars apparently decrease perceptibly in transverse diameter from anterior to posterior if KU10203 with associated $M^1$ and $M^2$ is reliable.




FIGURES 102-114. *Proheteromys sulculus.*——102, Right $P^4$, KU10207.——103, Right $P^4$, KU10210.——104, Right $P^4$, KU10211.——105, Left $P^4$, KU10213.——106, Left $P^4$, KU10215.——107, Right $P^4$, KU10214.——108, Right $M^1$-$M^2$, KU10205.——109, Right $M^3$, KU10209.——110, Right $P_4$, KU10225.——111, Right $D_m$, KU10220.——112, Left $P_4$-$M_2$, KU10217.——113, Right $M_3$, KU10219.——114, Type specimen, left ramus with $P_4$-$M_2$, KU10203; 114a, medial view; 114b, occlusal view of $P_4$-$M_2$; 114c, lateral view. [Figs. 102-107, 113, ×9; Figs. 108-112, 114b, ×10; Figs. 114a, 114c, ×5.]

All of the fourth upper premolars assigned to *Proheteromys sulculus* have a three-cusped metaloph and a one-cusped protoloph. The presence of only one cusp on the protoloph is in contrast to the Heteromyinae generally (see diagnosis of that subfamily by WOOD, 1935, p. 165), but the difference may be explained by assuming that in *P. sulculus* additional cuspules have not yet developed. Even with wear, as long as any cusp development remains evident, the protocone seems not to be connected posteriorly to the metaloph. Instead, connection is made usually by way of the entostyle thus giving rise to an incipient J-pattern (WOOD, 1935, p. 168). A variation from this connection is seen in $P^4$ of the skull fragment, KU10204, and one other $P^4$, KU10213, in which the protocone remains isolated, but the tendency toward internal connection is much commoner.

The first upper molar is represented by two teeth, KU10216 and KU10205, not differing much from each other. The styles are well developed, there is a short anterior cingulum, and first union of the two lophs is made at the lingual border. The two teeth differ in that in KU10216 the anterior cingulum is better developed, and the internal connection between lophs is better developed than in KU10205.

$M^2$, judging from KU10205, is smaller than $M^1$, and the styles are closer together. No anterior cingulum can be observed in this specimen. KU10212 may also represent the second molar. It is more worn than $M^2$ of KU10205, but the shape seems the same, and the pattern perhaps as nearly like that of $M^2$ as of $M^1$. The size of this tooth, however, strongly suggests that it is a first molar.

$M^3$ is known by a single tooth only, KU10209. In it the protoloph is composed of three cusps of which the most internal represents, presumably, the undivided cingulum. The large, externalmost cusp seemingly is subdivided near its apex into two, possibly three, cuspules. The posterior loph is obscurely divided into two cusps. Although there is a slight notch between the lophs externally, the cusps essentially form a ring around a central basin.

The lower jaw is known adequately from KU10203, and some parts of it are preserved in other specimens. The mental foramen is situated about midway between the alveoli for the incisor and for $P_4$. Posterior to the foramen is the anterior end of the masseteric crest. In KU10218, the anterior part of the crest is much more robust than in KU10203, and terminates a little more dorsally. This seems to be true also in KU10225. The angular process of the jaw is somewhat attenuated; possibly more as in that of *Perognathus* than *Heteromys*. There is no pit or depression between $M_3$ and the ascending process of the lower jaw.

The lower incisor is somewhat flattened on its anterior face.

In $P_4$ all four principal cusps are well-developed (mesoconid, protoconid, entoconid, and hypoconid of the WOOD nomenclature, 1935, p. 79). The outer pair (mesoconid and hypoconid) are somewhat closer together than the inner one. No X-pattern is present. A small anteroconid lies between the mesoconid and protoconid, but closer to the mesoconid to which it is actually joined. A small hypostylid is present on the metalophid. Between the hypoconid and entoconid is what GALBREATH (1953, p. 98) has described as a hypoconulid. Each of two other specimens (KU10217, KU10225) has a $P_4$ and with KU10203 indicate considerable individual variation of this tooth in *Prohetero-*

*mys sulculus*. KU10217 differs from KU10203 in: (1) smaller anteroconid and hypostylid; (2) no discernible hypoconulid; and (3) probably, anterior pair of cusps closer together. KU10225 departs still farther in the apparent absence of the anteroconid, but the heavier wear on this specimen compared with the other two may possibly be responsible for this difference. Neither is a hypostylid present, but the somewhat acute end of the hypolophid suggests its obliteration by wear. In the relatively great depth of the internal and external parts of the transverse valley of $P_4$ in respect to its middle, KU10225 has a faint suggestion of the start of an X-pattern, which the other two specimens do not possess.

KU10220 seems to be the deciduous lower premolar of *Proheteromys sulculus*. Four principal cusps correspond to the four cusps of the permanent premolar. The mesoconid is noteworthy in being set external to the hypoconid and in its more pyriform, less oval section. Hypoconid and entoconid are united by a low crest extending anteriorly between the other two cusps in more or less of an X-pattern. An anteroconid occupies an anteromedian position on the crown. Three accessory cingular cuspules are present; the largest is on the posterior border of the tooth behind and nearly midway between the hypoconid and entoconid, and the two smaller cusps lie at the posteroexternal border of the tooth. One of them is at the posteroexternal angle of the tooth, and the other is more anterior and nearly opposite the hypoconid. This tooth is closest in construction in $Dp_4$ of *Microdipodops* (WOOD, 1935, fig. 33) and *Cupidinimus* (WOOD, 1935, fig. 40), but differs considerably even from these in the position of the mesoconid, which is at the external border of the tooth rather than internal to an external cingulum. Unfortunately, no deciduous lower molars of fossil heteromyines are otherwise known.

The crown of $M_1$ shows four prominent cusps that are paired to form distinct anterior and posterior lophs. External to them are cingular structures that nominally complete the bilophed, six-cusped pattern of typical heteromyids. The hypostylid, however, is usually small in comparison to the hypoconid and entoconid cusps and tends to be united with the external structure in front. What may be loosely termed the protostylid is large, but seems to consist of a clearly cingular ridge extending from the anterior face of the protoconid around the anteroexternal border of the tooth nearly to the transverse valley; at this point it swells into a small cusp that may be here termed as the true protostylid. The hypoconid especially, but also the entoconid, tends to be elliptical in section with its major axis directed toward the middle of the transverse valley, and hence the tooth develops with wear a pattern suggesting the beginnings of an H-pattern (WOOD, 1935, p. 88). As a result of this incipient H-pattern and the weak union of the stylar structures, wear tends to isolate the external part of the transverse valley as an enamel basin. In other specimens, such as KU10217, the separation of hypostylid and entostylid is more pronounced, and the hypoconid and entoconid have more transverse alignments. The H-pattern is hardly or not at all developed. Separation of specimens, however, can not be consistently made on the basis of these differences in pattern.

$M_2$ is approximately the size of $M_1$, being smaller in KU10217 and larger in KU10203 than the latter. Although specimens are not sufficient for clear demonstration, it seems that the second molar tends to have a smaller hypostylid, a less distinctly cusplike termination of the protostylid structure, and to show less of an H-pattern. It is not possible to identify more than tentatively $M_1$ and $M_2$ when these teeth occur isolated from the jaw. Either $M_1$ or $M_2$ or both may occasionally have vestiges of a posterior cingulum. $M_1$ and $M_2$ seem to approach in pattern those of *Heliscomys* (WOOD, 1935, p. 82) and *Florentiamys* (WOOD, 1936).

$M_3$ is represented by two isolated teeth, KU10219 and 10226. Judging from the alveolus for the third molar present in KU10203, this tooth is relatively of large size. In KU10219, the protostylid can hardly be described as more than a thick, raised cingulum beginning on the anterior face of the tooth and terminating at the base of the metalophid. A hypostylid is not present. In KU10226, the "protostylid" is clearly describable only as a cingulum. This cingulum extends more posteriorly than in 10219 and terminates opposite the hypoconid as a most minute "hypostylid."

In all three lower molars, the pattern is clearly based on anterior and posterior crests, each composed of two cusps, together with an external cingulum. As stated by GALBREATH (1953, p. 98), *Proheteromys sulculus* represents a stage structurally intermediate between *Heliscomys* and the later heteromyids, especially those ascribed to *Proheteromys*. They are, in fact, almost what one would expect in an early Miocene stage of evolution.

*Comparisons*. Most of the known contemporary or near contemporary species of heteromyids are excessively fragmentary or far removed geographically from *Proheteromys sulculus*, or both. *P. matthewi* (WOOD, 1935, p. 170), known only from a lower jaw with $P_4$-$M_1$ from the upper Rosebud of South Dakota, perhaps is contemporary with *P. sulculus*, and at the same time is not geographically remote. These two species agree in size, but *P. matthewi* lacks accessory tubercles on $P_4$. The structure of $P_4$ of *P. matthewi* is close to that described below in a specimen referred to *Mookomys* sp. cf. *M. formicorum*. If KU10234 were to be referred to *P. sulculus*, the two species could not be distinguished on known materials, but the normal $P_4$ of *P. sulculus* is clearly different from that of the type of *P. matthewi*. *M. formicorum* (WOOD, 1935, p. 89), known only from three isolated teeth, is from the lower Harrison of Nebraska and hence older than *P. sulculus*. *M. formicorum*

is also of the same size as *P. sulculus* but $P^4$ seemingly lacks any suggestion of a J-pattern, and the structure of the lower molar is different in its more perognathine appearance. *P. floridanus* (WOOD, 1935, p. 166; 1947, p. 489), from possible partly contemporary, partly later beds, seems closely to resemble *P. sulculus* in many features but is smaller, and $P_4$ is more definitely heteromyine. *P. thorpei* (WOOD, 1935b, p. 368) of the John Day differs in structure of $P_4$ (mesoconid low, not clearly separate from hypostylid) as well as in its older age, and *M.? bodei* (WILSON, 1949a, p. 58) of the Sespe is larger and certainly older geologically.

Assignment of the species *sulculus* to *Proheteromys,* rather than to *Mookomys,* is made because, with one exception, the features of *P. sulculus* are those cited by WOOD (1935) as characteristic of the Heteromyinae or found in the Heteromyinae when not characteristic. The exception is the weakly sulcate upper incisors of *P. sulculus.* Those of *Proheteromys* are described as asulcate, but grooving probably similar to that of the Quarry A species is found in *Diprionomys* (WOOD, 1935, p. 179), a heteromyine, and the grooving presumably present in *Mookomys* is deeper.

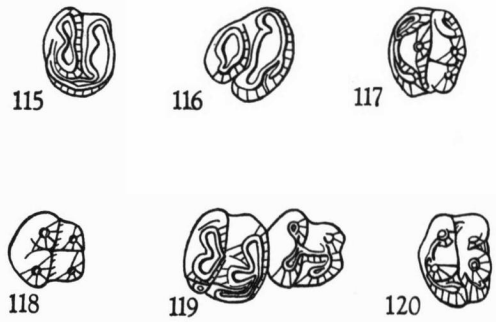
WOOD has suggested that *Mookomys* possibly passed through a *Proheteromys* stage (1937, p. 215-216). If such were actually the case, *M. formicorum* is readily transferable to *Proheteromys.* WOOD (1935, p. 90) remarks that there is no really outstanding reason why *M. formicorum* should not be referred to the Heteromyinae and all early Miocene species could be regarded as representing one broad genus, *Proheteromys.* At any rate, I suspect that several of the features thought of as characteristic of *Proheteromys* and the Heteromyinae, or of *Mookomys,* are simply primitive features retained in one or the other line. It is also, I think, reasonably evident that Heteromyinae and Perognathinae are not clearly separable at this stage of the Miocene (*M.? bodei*; heteromyid, prob. n. gen., n. sp., JAHNS, 1940, p. 178, 182; as well as the present specimens, all show cross-over characteristics).

*Measurements of* Proheteromys sulculus, *in Millimeters*

| | | | |
|---|---|---|---|
| $P^4$, ap | 1.0-1.4 | $P_4$, ap | 0.8-0.9 |
| tr | 1.1+-1.3 | tr | 0.8-1.0 |
| $M^1$, ap | 1.0 | $M_1$ and $M_2$, ap | 0.9-1.1 |
| tr | 1.2 | tr | 1.0-1.2 |
| $M^2$, ap | 0.7-0.9— | $M_3$, ap | 1.0 |
| tr | 1.0+-1.2 | tr | 1.0-1.0+ |
| $M^3$, ap | 0.6+ | | |
| tr | 0.8 | | |

**FLORENTIAMYS? sp.**
Figure 115

An upper molar ($M^1$ or $M^2$), KU10231, approaches the pattern of upper molars of *Florentiamys loomisi* (WOOD, 1936), from the early Miocene of Wyoming, although KU10231 is considerably smaller. The only observable difference between the two is the slightly shorter anterior cingulum in my specimen. One or two other specimens from Quarry A, however, suggest somewhat intermediate stages between KU10231 and specimens of *P. sulculus,* and it is conceivable that KU10231 is an extreme variant of the latter. On the other hand, if KU10231 does represent *Florentiamys,* it probably represents a new species of that genus. In either case, the specimen serves to emphasize the point that *Florentiamys* is much less unusual as a heteromyid than originally thought.




FIGURES 115-120. *Florentiamys ?* and *Mookomys.*———115, *Florentiamys?* sp., Left $M^1$ or $M^2$, KU10231.———116-120, *Mookomys* sp., cf. *M. formicorum.*———116, Left $P^4$, KU10232.———117, Left $M^1$ or $M^2$, KU10133.———118, Left $P_4$, KU10234.———119, Right $P_4$-$M_1$, KU10235.———120, Left $M^1$ or $M^2$, KU10233. [Figs. 115, 116, 119, 120, ×10; Figs. 117, 118, ×9.]

**MOOKOMYS sp. cf. M. FORMICORUM Wood, 1935**
Figures 116-120

Several specimens from Quarry A differ from those referred to *Proheteromys sulculus* to such a degree that I have accorded them separate designation. These are: $P^4$, KU10232; upper molars, KU10233; $P_4$, KU10234; and jaw fragment bearing $P_4$-$M_1$, KU10235. It is not, however, beyond possibility that they are extreme variants of *P. sulculus.*

These teeth, taken collectively, suggest an animal with dentition approximately the size of that of *Proheteromys sulculus,* but slightly more robust.

The fourth upper premolar, KU10232, differs from that of *Proheteromys sulculus* in the presence of a small external cusp (the paracone?), and the absence of any connection of protoloph to metaloph even after considerable tooth wear. A short posterior cingulum is present.

Two upper molars, KU10233, both have a transverse valley sharply separating protoloph and metaloph even at the internal margin. A short strip of anterior cingulum is present in one. Characteristically, cingular ridges extend from entostyle and from metacone to unite behind

the hypocone. There is a marked resemblance in pattern to that of CM10177 of *Mookomys formicorum* (WOOD, 1935, fig. 8b), the holotype of that species. WOOD regards CM10177 as an $M_1$, whereas ours seemingly are upper molars.

KU10234 is a $P_4$ bearing a closer resemblance to that of *Proheteromys matthewi* than to that of *Mookomys altifluminus* (WOOD, 1935, p. 91—that of *M. formicorum* has not been described), if due allowance is made for difference in stage of wear. No accessory cusps are present in KU10234, and it is more robust than normal for a premolar of *P. sulculus*.

The final specimen, KU10235, arranged under the name *Mookomys* sp. cf. *M. formicorum* is a fragment of jaw bearing $P_4$ and probably $M_1$. [This tooth was broken out of the jaw at the time of discovery, and conceivably could be an $M_2$.] A part of the masseteric scar is preserved, and it seems relatively weak as compared with that of *P. sulculus;* it terminates closely behind the mental foramen. The incisor has a more rounded face than in the type of *P. sulculus*. $P_4$ more closely approaches the X-pattern (WOOD, 1935, p. 88) of the Perognathinae than do any of the specimens referred to *P. sulculus*. Short crests from the hypoconid and metaconid unite and extend forward between the protoconid and mesoconid. No accessory cuspules are present. $M_1$ is like that of *P. sulculus* in pattern.

The open assignment given above is mostly for convenience. Each of the specimens, save perhaps KU10234, however, has some point or points of resemblance to the Perognathinae or to *Mookomys,* and *M. formicorum* is the one available perognathine that is at all comparable in age.

*Measurements of* Mookomys *sp. cf.* M. formicorum, *in Millimeters*

| | | | |
|---|---|---|---|
| $P^4$, ap | 1.1 | $P_4$, ap | 1.0-to 1.0 |
| tr | 1.4— | tr | 1.0-1.0+ |
| $M^1$ or $M^2$, ap | 1.0 | $M_1$, ap | 1.0+ |
| tr | 1.25-1.3 | tr | 1.2 |

**PROHETEROMYS sp. cf. P. MAGNUS Wood, 1935**
Figures 121-125

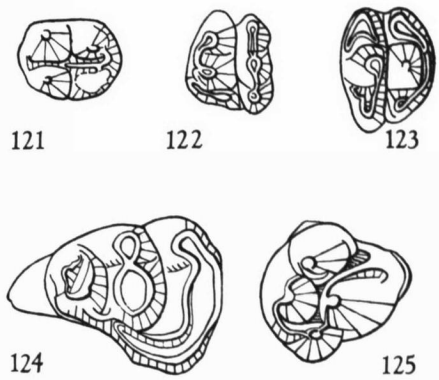
Whatever the status of the specimens assigned to *Mookomys* sp. cf. *M. formicorum* and to *Florentiamys?* sp., it is clear that at least one species in addition to *Proheteromys sulculus* occurs at Quarry A. This is a much larger one than *P. sulculus* and seemingly is related to, though not identical with, *P. magnus* (WOOD, 1935, p. 168; 1947, p. 490) of the Florida Miocene. Unfortunately, it is represented by only five isolated cheek-teeth, the same number of teeth as in the described material from Florida.

*Proheteromys magnus* is one of the larger species of heteromyid, and the Quarry A species is nearly the same in size. The following table shows this.

*Measurements of Species of* Proheteromys, *in Millimeters*

| | *P. magnus* | *P.* sp. cf. *P. magnus* |
|---|---|---|
| $P^4$, ap | 1.6 | 2.0 |
| tr | 1.9 | 2.0 |
| $Dp^4$, ap | 1.4 | 2.4 |
| tr | 1.4 | 2.1 |
| $\underline{M}$, ap | ..... | 1.25 |
| tr | ..... | 1.6 |
| $P_4$, ap | ..... | 1.4 |
| tr | ..... | 1.2 |
| $\underline{M}$, ap | 1.5 | ?1.3 |
| tr | 1.5-1.7 | ?1.4— |

The teeth seem not much, if any, higher-crowned than in *Proheteromys sulculus.*




FIGURES 121-125. *Proheteromys* sp. cf. *P. magnus.*————121, Right $P_4$, KU10239.————122, Left $M_1$ or $M_2$, KU-10240.————123, Right $M^1$ or $M^2$, KU10238..————124, Left $D^m$, KU10237.————125, Right $P^4$, KU-10236. [Figs. 121, 124, 125, ×9; Figs. 122, 123, ×10.]

A fourth upper premolar, KU10236, can be compared directly with the type of *Proheteromys magnus.* At first sight, there seems to be considerable difference in the pattern. The $P^4$ of *P. magnus* is described as 5-cusped whereas the Quarry A specimen is 4-cusped. The type is from a locality (Fullers Earth Co. Mine, Midway) of probably later age, but the additional cusp is a large one, and the alignment of cusps in the posterior loph is rectilinear rather than curving. Study of *P.* sp. cf. *P. magnus, P. magnus,* and *P. sulculus* has convinced me that WOOD has misidentified the cusps in $P^4$ of *P. magnus,* and that their "correct" identification reduces the distinctions to no more than one might expect with the age differences concerned. *P.* sp. cf. *P. magnus* seems altogether comparable to *P. sulculus* in fundamental cusp structure of $P^4$, but differs in its larger size, a somewhat more crested condition of the cusps, and a deeper transverse valley. Moreover, unlike the premolars of *P. sulculus,* those of *P.* sp. cf. *P. magnus* have a ridge from the protocone leading outward to the base of the crown where it is expanded into a cusplike cingular edge. The anterior loph consists of the protocone only; the posterior

loph consists of metacone, hypocone, and an anteriorly placed entostyle. The entostyle is connected to the hypocone by a crest that is bulging in incipient cusp fashion. I think it is this bulge, expanded, that WOOD has called the entostyle in *P. magnus,* and that the entostyle has been termed the protostyle. The relative size and position of the cusps in $P^4$ of *P. magnus* seem to be in conformity with this interpretation, and the presence of a large protostyle in $P^4$, in this position, is most unusual. Wood mentions another $P^4$ of *P. magnus* (FSGS V-5335) which he states, "is more advanced in the closer relationship of the protostyle and the entostyle" (p. 47, 1932). This may in fact be a closer approach to KU10236.

KU10237 is a $Dp^4$, probably to be assigned to *Proheteromys* sp. cf. *P. magnus.* The pattern consists of two cusps in the posterior row, two in the middle, and one in the anterior row. The inner one of the paired cusps is the larger. A heavy cingular ridge extends from the posterointernal cusp forward to the transverse valley separating the anterior cusp from the median row, or slightly beyond, terminating as a small swelling on the side of the anterior cusp. KU10237 seemingly differs in pattern from that of FSGS V-5336 regarded by WOOD as representing $Dp^4$ of *P. magnus.* The latter is much more nearly like the permanent premolar than is KU10237, and was originally regarded by WOOD (1932, p. 48) as representing the $P^4$ of a species other than *P. magnus.* FSGS V-5336 is smaller than the permanent premolar which replaces it whereas KU10237 is larger than its supposed replacement. Generally, the deciduous premolars in heteromyids are larger in transverse diameter than the permanent premolars, a point in favor of my assignment. If KU10237 does not pertain to *P.* sp. cf. *magnus,* it probably is the $Dp^4$ of an entoptychine.

The first or second upper molar is probably represented by KU10238. This tooth seems not to be represented by material of *Proheteromys magnus* of Florida, although there are points of resemblance to the lower molar, FSGS V-5333, figured by WOOD (1935, p. 168, fig. 94) in the construction of the posterior cingula and the large size of the central cusp in the lophs. In KU 10238 both protoloph and metaloph are alike except for anteroposterior reversal of structures. In each there are three cusps, the central one being the largest. Short cingular crests from the protostyle and paracone converge forward toward the protocone, and converge backward from the entostyle and metacone toward the hypocone. Both entostyle and protostyle are anteroposteriorly compressed and nearly riblike structures.

A large $P_4$, KU10239, is probably to be referred to the same species as the upper teeth. Except for its larger size and a greater separation of posterior cusps, it resembles $P_4$ of *Mookomys* sp. cf. *M. formicorum,* especially in possessing the same low crest running from the posterior cusps forward and terminating between the anterior cusps. No $P_4$ of *Proheteromys magnus* has been described. The structure of KU10239 is not that to be expected in a representative of the genus *Proheteromys.* However, the original reasons for assigning *P. magnus* to the genus are no longer so pertinent as they were (for example, the presence of anterior or posterior cingula on the cheek-teeth).

KU 10240 is a lower molar seemingly too large for reference to *Mookomys* sp. cf. *M. formicorum,* although rather small for assignment to *Proheteromys* sp. cf. *P. magnus.* In any case, it exhibits no special peculiarities in its pattern. Hypostylid, hypoconid, and entoconid form a straight line of cusps, and the transverse valley is relatively deep even at the external margin. Consequently, there would be little tendency to isolate with wear the external part of the valley as a basin.

These teeth (with the possible exception of KU10240) are decidedly large for a heteromyid, and for this reason I think it is reasonable to regard them as representing a single species. They are in fact not much smaller (certain measurements are not at all smaller) than some teeth of the entoptychine *Pleurolicus* (WOOD, 1936a, p. 29-30). Entoptychines are, moreover, recorded from the Martin Canyon local fauna. $P^4$, especially, could be entoptychine, although seemingly too short-crowned. In the absence of skull material, and especially with fragmentary dental material, it is not clear to me how a definite assignment to either Entoptychinae or Heteromyidae is always to be reached.

*Comparative Measurements of Heteromyid Species, in Millimeters*

| | *P.* sp. cf. *P. magnus* | *M.* sp. cf. *M. formicorum* | *P. sulculus* | *P. matthewi* |
|---|---|---|---|---|
| $P^4$, tr | 2.0 | 1.4- | 1.1+-1.3 | ..... |
| $M^1$, ap | 1.25(a) | 1.0(a) | 1.0 | ..... |
| tr | 1.6(a) | 1.25-1.3(a) | 1.2 | ..... |
| $M^2$, ap | ..... | ..... | 0.7-0.9- | ..... |
| tr | ..... | ..... | 1.0+-1.2 | ..... |
| $P_4$, ap | 1.4 | 1.0-to 1.0 | 0.8-0.9 | 1.0 |
| tr | 1.2 | 1.0-1.0+ | 0.8-1.0 | 1.0 |
| $M_1$, ap | ?1.3(b) | 1.0+(b) | 0.9+-1.1(b) | 1.14 |
| tr | ?1.4-(b) | 1.2(b) | 1.0-1.2(b) | 1.14 |

| | *M. formicorum* | *P. floridanus* | *P. thorpei* | *P. magnus* |
|---|---|---|---|---|
| $P^4$, tr | 1.09 | ..... | ..... | 1.9 |
| $M^1$, ap | ..... | 0.78-0.84 | ..... | ..... |
| tr | ..... | 1.12-1.13 | ..... | ..... |
| $M^2$, ap | ..... | 0.74-0.80 | ..... | ..... |
| tr | ..... | 0.96-1.08 | ..... | ..... |
| $P_4$, ap | ..... | 0.71 | 0.94 | ..... |
| tr | ..... | 0.60 | 0.96 | ..... |
| $M_1$, ap | 0.94 | 0.78-0.85 | 1.16 | ..... |
| tr | 1.23 | 0.92-0.94 | 1.23 | ..... |
| $M_2$, ap | 0.90 | 0.88 | ..... | 1.5 |
| tr | 1.13 | 0.92 | ..... | 1.5-1.7 |

(a) Or $M^2$.
(b) Or $M_2$.

## Subfamily ENTOPTYCHINAE

The subfamily Entoptychinae, as now defined, contains representatives of the Geomyidae, Heteromyidae, or both; to it are assigned a few isolated teeth from Quarry A and better specimens in deposits of Marslandian age near the quarry. These specimens are now being studied by Dr. E. C. GALBREATH.

## Superfamily DIPODOIDEA

## Family ZAPODIDAE

Two species of zapodids, here referred to two different subgenera, are present in the fauna. The smaller and less common species seems to be referable to the Old-World genus *Plesiosminthus*. If so, this is the latest occurrence of the genus to be put on record. The second species seemingly is related to *Schaubeumys,* a closely related subgenus (or genus) if assignment of my material is correct. Authoritative records of *Schaubeumys* are restricted to a few localities only in the Plains area; the Asiatic species *Schaubeumys aralensis* ARGYROPOLO and *S. woodi* ARG. are cricetids, according to STEHLIN & SCHAUB (1951, p. 367). The New-World record of *Plesiosminthus* is so far unique.

Structurally, both *Plesiosminthus* and *Schaubeumys* are sicistines (striped mice), the most primitive of the dipodoid groups. Phylogenetically, they might be aberrant, or ancestral to some other zapodid group.

### PLESIOSMINTHUS (PLESIOSMINTHUS) CLIVOSUS Galbreath, 1953

Figure 126

*Plesiosminthus? clivosus,* GALBREATH 1953 (p. 99).

GALBREATH in 1953 named as new and assigned tentatively to the Old-World genus *Plesiosminthus* a zapodid rodent from Quarry A, then known by a single specimen, the type. Although zapodid rodents have since been found to be relatively common in the Quarry A fauna, specimens referable to *P. (P.) clivosus* have remained rare. The additional specimens permit me to describe part of the upper dentition, and, I think, to ascertain that *P. (P.) clivosus* is without much doubt to be referred to *Plesiosminthus* VIRET (1929).

Specimens of *Plesiosminthus (P.) clivosus,* additional to the type, are: KU10242, right lower jaw having $M_1$ and $M_3$; KU10243, fragment of left lower jaw having $M_2$-$M_3$; KU10244, left $M_2$ in jaw fragment; KU10245, right upper jaw having $P^4$-$M^1$; KU10246, right $M^1$ in jaw fragment; KU10247, right jaw fragment having worn $M^1$ and alveolus for $P^4$; KU10248, left upper jaw having $M^1$ and alveoli for $M^2$-$M^3$; KU10247, upper incisors. It is odd that the number of fragments of upper jaw and lower jaw should be equal. Usually upper jaws are distinctly in the minority, but the upper teeth seem all to be referable to *Plesiosminthus* rather than to some kind of cricetid or eomyid.

In *Plesiosminthus (P.) clivosus* the zygomatic arch takes origin distinctly anterior to the edge of $P^4$ as in *Zapus,* rather than as in *Sicista.* In this respect, *P. (P.) clivosus* resembles *P. (P.) myarion* of the European Aquitanian (SCHAUB, 1930, p. 618).

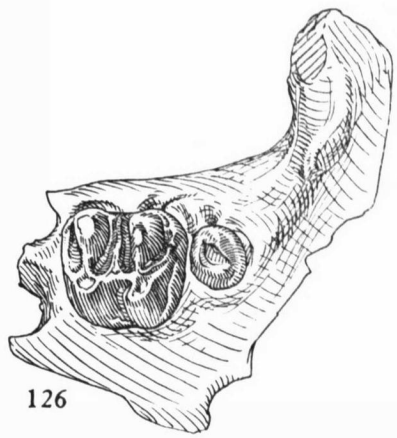



FIGURE 126. *Plesiosminthus (Plesiosminthus) clivosus.* Right upper jaw fragment with $P^4$-$M^1$, KU10245, ×17.

$P^4$ is a small tooth; its crown is hardly larger in diameter than that of the thick root. The crown consists of a principal cusp, anteroexternal in position, and a cingulum that borders the crown on the posteroexternal, posterior, internal, and anterointernal surfaces. The posteroexternal end of the cingulum bears a minute cuspule. The tooth is implanted obliquely, and consequently the crown is tipped back toward the first molar.

$M^1$ does not differ essentially from that described and figured for *Plesiosminthus myarion* (SCHAUB, 1930). $M^1$ is three-rooted, the internal root being undivided.

Although not in positive association, upper incisors are known that are of an appropriate construction to pertain to *Plesiosminthus* and *P. (P.) clivosus.* This material was noted by GALBREATH (1953, p. 99), but I think it can be more positively asserted now that the incisors are correctly assigned. More extended treatment will be given under the zapodid species to be described next.

The lower jaw and dentition of *Plesiosminthus (P.) clivosus* has been described by GALBREATH (1953) and *Plesiosminthus* of Europe also has been well described and figured (SCHAUB, 1930; STEHLIN & SCHAUB, 1951). Only a few points, mainly those made available by the new material, will be mentioned.

Although GALBREATH did not so state, there is a foramen between $M_3$ and the ascending ramus in the type. Its position seems to be the same as in *Plesiosminthus (P.) myarion,* although the foramen in *P. (P.) clivosus* possibly is smaller. In KU10243, the foramen is present but is more anterior in position. The lower incisor is

present in KU10242. It is a compressed tooth having a rounded enamel face.

In $M_1$, the anteroconid (paraconid of SCHAUB, 1930) is small in both available specimens, and set close to the trigonid cusps, but in KU10242 it is less median, more external, in position than in the type, and a cingulum extends inward to the metaconid.

In $M_2$, the postentoconid valley may be less enclosed than in *Plesiosminthus (P.) myarion*. KU10243 has no metalophulid II connection, but instead a spur directed toward the mesolophid.

In $M_3$, the mesolophid is stronger than on the type in both KU10242 and KU10243. Moreover, although the trigonid pit is present in these specimens it seems to be closed behind by a connection between mesolophid and metaconid rather than by the posterior arm of the protoconid. This connection in $M_3$ and the spur in $M_2$ suggest the start of complications leading to the crown pattern of *Pliozapus* (WILSON, 1936) (and *Sicista*).

The lower molars are all two-rooted.

GALBREATH (1953, p. 99) in his diagnosis of the species *Plesiosminthus (P.) clivosus* lists distinctions that are now seen to be difficult of application. In fact, I do not think that any of them hold in distinguishing all of our specimens from all of those of both *P. (P.) myarion* and *P. (P.) schaubi*. The characters that do seem the most valid are of a synthetic nature in respect to the European specimens, and for this reason I think that *P. (P.) clivosus* is properly to be assigned to *Plesiosminthus*. As a matter of fact, there is some difficulty in finding reliable characters to separate *P. (P.) clivosus* from *P. (P.) myarion*.

*Comparisons.* The species to which *Plesiosminthus (P.) clivosus* is closest is *P. myarion* of the European Aquitanian. Differences real and apparent are as follows: (1) in *P. (P.) clivosus,* hypocone and protocone seem less obliquely compressed on the average; (2) in *P. (P.) clivosus,* the anteroconid of $M_1$ is small and variable but more separate from than connected to protoconid, whereas in *P. (P.) myarion* the anteroconid is seemingly larger and more definitely joined with the protoconid; (3) *P. (P.) clivosus* may have a more open postentoconid valley in $M_2$; (4) in *P. (P.) clivosus,* some specimens show a tendency to develop a kind of metaconid-mesolophid union that seemingly is absent in *P. (P.) myarion*. Sufficient variation is present in the specimens of both species to make formal diagnosis difficult.

*Plesiosminthus (P.) clivosus* is perhaps more clearly distinct from *P. (P.) schaubi* of the Stampian. For example: (1) the tooth row of *P. clivosus* is more posterior in position in respect to the root of the zygomatic arch than in *P. (P.) schaubi;* and (2) the posterior half of $M_3$ in *P. (P.) clivosus* is not so simplified and the tooth is longer than in *P. (P.) schaubi* (at least in the type specimens of each). The American species may more nearly resemble *P. (P.) schaubi* than *P. (P.) myarion* in lesser compression of protocone and hypocone.

*Plesiosminthus (P.) promyarion* is not well enough known for effective comparison, but its older age (Stampian) and considerable geographic separation argue against any possibility that the two could not be distinguished under more favorable conditions. For example, LAVOCAT (1951, p. 45) refers to *P. (P.) promyarion* a specimen from Cournon in which $M_2$ lacks the union of posterior arm of protoconid with metaconid displayed in *P. (P.) clivosus*.

*Plesiosminthus bavaricus* has been named by FREUDEN-

*Comparative Measurements of* Plesiosminthus, *in Millimeters*

| | *P. clivosus* | *P. galbreathi* | *P. grangeri* | *P. sabrae* | *P. asiae-centralis* | *P. tangingola* | *P. parvulus* | *P. myarion* |
|---|---|---|---|---|---|---|---|---|
| $P^4$-$M^1$ | 1.5 | 2.0-2.1 | ..... | ..... | 2.3 | 1.8 | ..... | ..... |
| $M_1$-$M_2$ | ..... | 2.7 | ..... | ..... | 3.4 | 2.5 | 1.9 | ..... |
| $P^4$, ap | 0.5 | 0.7-to 0.7 | ..... | 0.55(a) | 0.7 | 0.5 | 0.4 | ..... |
| tr | 0.6— | 0.8-0.9 | ..... | 0.65(a) | 0.85 | 0.6 | 0.5 | ..... |
| $M^1$, ap | 1.0-1.25 | 1.4-1.5 | 1.55 | 1.20-1.37 | 1.7 | 1.15-1.3 | 0.95-1.1 | ..... |
| tr | 1.0-to 1.1 | 1.3-1.5 | 1.40 | 1.15-1.35 | 1.7 | 1.05-1.2 | 0.8-1.1 | ..... |
| $M^2$, ap | ..... | 1.3+ | ..... | 1.42 | 1.65-1.7 | 1.2-1.3 | 0.9-1.1 | ..... |
| tr | ..... | 1.35 | ..... | 1.43 | 1.4-1.6 | 1.1-1.2 | 0.75?-1.0 | ..... |
| $M^3$, ap | ..... | 1.0 | ..... | ..... | 1.2 | ..... | 0.75-0.8 | ..... |
| tr | ..... | 1.1 | ..... | ..... | 1.3 | ..... | 0.75 | ..... |
| $M_1$-$M_3$ | 3.0-to 3.1— | 3.9 | ..... | ..... | 3.9 | ..... | 2.6-2.8 | 3.0-3.5 |
| $M_1$-$M_2$ | ..... | 3.0 | ..... | ..... | 2.7 | ..... | 1.85-2.0 | ..... |
| $M_2$-$M_3$ | 2.25 | 2.6-2.7 | ..... | ..... | 2.6 | ..... | 1.6-2.0 | ..... |
| $M_1$, ap | 1.1-1.2 | 1.3-1.6 | 1.55 | 1.28-1.34 | 1.3-1.8 | 1.2-1.4 | 0.9-1.1 | ..... |
| tr | 0.8-1.0 | 1.0-1.2 | 1.20 | 0.97-1.04 | 1.1-1.35 | 0.85-1.1 | 0.65-0.8 | ..... |
| $M_2$, ap | 1.1-1.25 | 1.3-to 1.5 | 1.50 | 1.23-1.32 | 1.4-1.5 | 1.25-1.35 | 0.85-1.1 | ..... |
| tr | 1.0 | 1.1-1.25 | 1.23 | 1.10-1.12 | 1.1 | 0.9-1.1 | 0.7-0.85 | ..... |
| $M_3$, ap | 0.9-1.0 | 1.2-to 1.2 | 1.30 | 1.03 | 1.2-1.65 | 1.05 | 0.7-0.75 | ..... |
| tr | 0.8-1.0— | 1.0-1.0+ | 1.14 | 0.91 | 1.0-1.15 | 0.8 | 0.7 | ..... |

(a) Mean measurements (from BLACK, 1958).

BERG from the Chattian of Gaimersheim bei Ingolstadt (1941). Whatever be the status of this species, the illustrations are inadequate for comparisons with *P. (P.) clivosus*. The size range is the same as for *P. (P.) myarion*. FREUDENBERG states that in $M_1$ the anteroconid is isolated, and the mesoconid very weak, and that in $M_3$ the entoconid is not developed. In *P. (P.) clivosus* the mesoconid is distinct in the type, but less so in the other available specimen. Distinctness of entoconid in $M_3$ is variable in the three known specimens, but this cusp is obviously present in the type specimen.

BOHLIN (1946) named and described from the late Oligocene of Taben-buluk, Western Kansu (NW. China), three new sicistines assigned to his new genus, *Parasminthus*. He states (p. 15) that he, "hesitated much before creating a new genus" because of the striking agreement of his species with those of *Plesiosminthus*. The associated upper incisors, however, lacked the characteristic grooving of *Plesiosminthus,* and he thought this justified establishment of a new name. *P. (P.) clivosus* differs from each of the three Asiatic species in several characters with no especial favoring of any one. Because the upper incisors of *P. (P.) clivosus* are grooved as in European species, I think detailed comparison not necessary. I may add, however, one other character in which *P. clivosus* differs from the three Asiatic species *Parasminthus asiae-centralis, tangingola,* and *parvulus*. The upper $M^1$ has an undivided internal root, whereas the same tooth in species of *Parasminthus* is figured as having two inner roots.

*Schaubeumys grangeri* (WOOD, 1935a) and *S. sabrae* (BLACK, 1958) are American zapodid species of somewhat comparable age to *Plesiosminthus (P.) clivosus*. They are distinct, however, in several characters as Black has shown. Extended discussion is reserved for the following species.

### PLESIOSMINTHUS (SCHAUBEUMYS) GALBREATHI Wilson, n.sp.

Figures 127-131

This species is named in honor of Dr. EDWIN C. GALBREATH, colleague for many years in the work in northeastern Colorado.

*Holotype.* Fragmentary left jaw having $M_1$-$M_3$, No. 10250, Univ. Kansas Mus. Nat. Hist.

*Referred specimens.* KU10251, right maxillary having $P^4$-$M^1$; KU10252, left maxillary having $P^4$-$M^1$; KU10253, left maxillary having $M^1$-$M^2$; KU10254, left $M^1$; KU10255, left $M^3$; KU10257, fragmentary right lower jaw having $M_1$-$M_2$; KU10258, fragmentary right lower jaw having $M_2$-$M_3$; KU10259, fragmentary right lower jaw having $M_2$-$M_3$; KU10260-KU10264, isolated first lower molars; KU10265, fragment of jaw having right $M_2$; KU10266-KU10269, isolated second lower molars; KU10256, upper incisors.

*Geological age and locality.* Sandy silts of late Arikareean age in the Pawnee Creek Formation, Quarry A, NE¼ sec. 27, T. 11 N., R. 53 W., Logan County, Colorado.

*Diagnosis.* Approximate size of *Plesiosminthus (Schaubeumys) grangeri,* but possibly averaging smaller; averaging larger than *P. (S.) sabrae*. $P^4$ with principal cusp which is relatively median in position. Anterior face of hypocone of $M^1$ rounded rather than flat. Anteroconid of $M_1$ present, but small, usually somewhat external rather than median in position, close to trigonid cusps. Anteroconid of $M_2$ united with protoconid. Postentoconid valley of $M_3$ usually enclosed by curving posterolophid which may on occasion be produced anteriorly as a bordering ridge extending to the metaconid; mesolophid of $M_3$ short in most. Greater (?) closure of postentoconid valley in all molars than in *P. (S.) grangeri*.

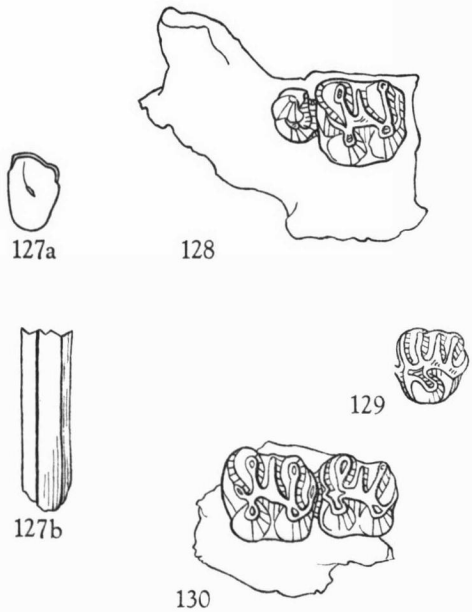
*Description.* No upper incisors have been found in direct association with parts of the upper jaws. Upper incisors here assigned to *Plesiosminthus (Schaubeumys)* may be of some other genus. But, isolated incisors are known which agree in almost all ways, save size, with those assigned to *P. (Plesiosminthus) clivosus* and have the characteristic structures of those allocated to European species of *Plesiosminthus*. Only a few of the other rodents known from Quarry A would have incisors of a size in harmony with those assigned to the zapodids. The eomyids, *Paradjidaumo* and *Adjidaumo* lack grooves in the upper incisors, and I am not aware that any eomyid has grooves. A heteromyid in the Quarry A fauna has incisors of about the size of those assigned to *P. (Schaubeumys)*. These incisors are distinctly different in structure from those of *Plesiosminthus* although having faint but broad grooves. Ungrooved incisors are also known covering a range of size that would include *Pseudotheridomys* and any heteromyid.

The upper incisors, KU10256, have a well-defined groove on the anterior face, and a second, smaller groove, or perhaps more accurately a raised border or rim, on the inner edge. The groove may be less sharply defined than that in *P. (P.) clivosus,* but the raised inner edge is more readily seen in *P. (S.) galbreathi*. The enamel overlaps the inner face of the incisor strongly in both species. This enamel is minutely furrowed, more readily seen in *P. (S.) galbreathi* than in *P. clivosus,* and is relatively thin, especially in the former.

A small part of the palate and zygomatic arch is preserved, and shows a relationship of tooth row to root of arch like that in *P. (P.) clivosus*. A distinction may exist in the angle between the base of the arch and the alveolar border of the tooth-row. In KU10245 of *P. (P.) clivosus,* the arch juts from the alveolar border abruptly, approximately at right angles. In *P. (S.) galbreathi,* the arch slants forward before curving laterad. A second specimen (KU10247) of *P. (P.) clivosus* suggests a condition more nearly like that in *P. (Schaubeumys),* but

the specimen is poorly preserved. Both American subgenera resemble *Zapus* rather than *Sicista* in position of the anterior end of the tooth-row.

The structure of $P^4$ is close to that in *Plesiosminthus (P.) clivosus*. The root is thick and slanting, and the crown relatively small and tilted. A principal cusp and surrounding cingulum is likewise present. The principal cusp seems to be more anteromedian in position, and the external cuspule may be better developed in *P. (S.) galbreathi*.




FIGURES 127-130. *Plesiosminthus (Schaubeumys) galbreathi.*————127, Right upper incisor, KU10256; 127a, cross-section; 127b, anterior view.————128, Fragment of left upper jaw with $P^4$-$M^1$, KU10252. ————129, Left $M^3$, KU10255.————130, Fragmentary left upper jaw with $M^1$-$M^2$, KU10253. [All ×9, except Fig. 129, ×10.]

Each upper molar of *P. (S.) galbreathi* is three-rooted; the undivided inner root is large and slightly grooved.

The first upper molar although conforming in pattern generally to that of *P. (P.) clivosus* exhibits some differences. In *Plesiosminthus (Schaubeumys) galbreathi* a pronounced embayment of the external wall of the tooth tends to divide the tooth into two parts of unequal transverse diameters, the anterior being the greater. *P. (P.) clivosus* lacks the pronounced infolding of the external wall, and both parts of the tooth are more nearly equal in diameter. The protocone and hypocone in *P. (S.) galbreathi* tend to be anteroposteriorly rather than obliquely compressed, and this has altered the shape of the internal embayment between these cusps accordingly. This embayment is U-shaped in *Schaubeumys,* and triangular in *Plesiosminthus*. The anterocone (or protoconule—it is a cusp on the protoloph whatever termed) is a distinct cusp, much more evident than in *P. (P.) clivosus*. SCHAUB has suggested that the upper molar of *P. (S.) grangeri* identified by WOOD as $M^2$ is in fact $M^1$ (STEHLIN & SCHAUB, 1951, p. 153). If this be so, then $M^1$ of *P. (S.) galbreathi* may differ from that of *P. (S.) grangeri* in the less oblique compression of the hypocone.

$M^2$, in the one available specimen, is smaller than $M^1$ with less pronounced bulge in the anterior half of the tooth. The anterocone (?protoconule) is indistinct, and the paracone is barely joined with the protocone, if at all.

$M^3$ has a construction closely resembling that of $M^3$ in European *Plesiosminthus*. In the clear separation of hypocone from protocone it seems less specialized than several specimens of *Plesiosminthus* figured by SCHAUB

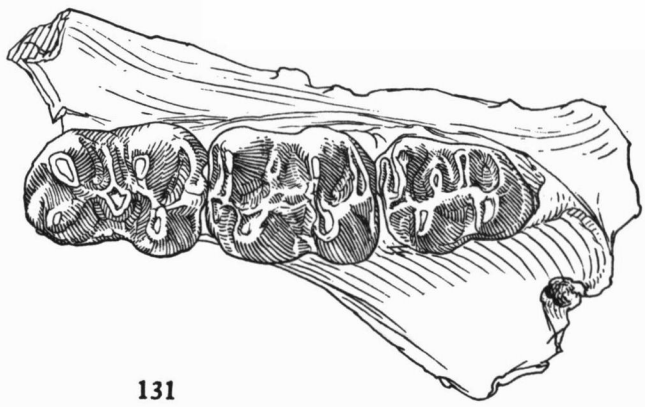



FIGURE 131. *Plesiosminthus (Schaubeumys) galbreathi.* Type specimen, left lower jaw with $M_1$-$M_3$, KU10250, ×18.

(1930, figs. 2, 5). A small, but distinct, anterocone (? protoconule) is present.

Although with rather limited scope for comparison, I can find no certain differences in the lower jaw or lower incisor in comparing *P. (Schaubeumys) galbreathi* with *P. (Plesiosminthus) clivosus*. In the type of *P. (S.) galbreathi,* a foramen lies between the ascending ramus and the hinder end of $M_3$. In KU10259 this foramen is reduced, whereas in KU10258 several minute foramina are visible, the most anterior being as far forward as the anterior end of $M_3$. A fragment of the rear end of a lower jaw is associated in the matrix with KU10264. Probably, but not certainly, the angular process of this fragment was like that in *Zapus*. The coronoid process is distinctly more developed, however, and more nearly like that of *P. (P.) myarion* figured (restored) by SCHAUB (1930, p. 623, fig. 9).

The construction of $M_1$ is essentially as in P. *(Plesiosminthus) clivosus*. The tooth on the whole, however, seems more cuspate, and less crested than in the latter.

This is especially evident in the posterolophid, which has a distinct hypoconulid whereas *P. (P.) clivosus* lacks this bulge. Probably also the postentoconid valley is broader and more widely open. The mesoconid may also be more centrally located, but this part of the tooth seems highly variable in several large populations of fossil zapodids and cricetids to which I have had access, and I suspect that the position of the mesoconid, and especially the orientation of the ectolophid varies much individually. The anteroconid of *P. (S.) galbreathi* probably differs but little from that in *P. (P.) clivosus*. In any case, considerable variation of this cusp exists in both. Seven specimens of $M_1$ of *P. (S.) galbreathi* are available, and the apparent variation of this cusp is worth describing. The anteroconid is always small and in two somewhat worn specimens (KU10261, KU10262) cannot be seen at all. KU10263 and KU10260 are unworn and show two small anteroconids in each, one internal and one external. In KU10257 an anteroconid is present adjacent to the protoconid with a connecting cingulum to the metaconid. In the type, also with anteroconid adjacent to protoconid and a low cingulum, the anteroconid and protoconid are seemingly not joined. In KU10264 the anteroconid is present and median.

In $M_2$ the hypoconulid is less distinct than in $M_1$, but is usually evident as a slight nick in the posterior surface of the posterolophid at the appropriate position. In general, $M_2$ of *P. (Schaubeumys) galbreathi* is to be distinguished from that of *P. (Plesiosminthus) clivosus* by lack of the metalophulid II connection with the metaconid present in the latter. The only connection normally present in $M_2$ of *P. (S.) galbreathi* is an anterior one by way of metalophulid I and the anteroconid cuspule. The posterior connection can exist, however, in *P. (S.) galbreathi* (KU10267, KU10265) and it seemingly can be absent in *P. (P.) clivosus*. None of the lower second molars of *P. (S.) galbreathi* has the peculiar construction of the type of *P. (S.) grangeri* in which the protoconid is isolated by a valley from the anteroconid and metaconid (WOOD, 1935a, fig. 1), but this condition is approached in individual specimens.

Only three third lower molars are available. The pattern is in general plesiosminthid. In KU10258 and 10250 the postentoconid valley is closed and there is no attachment of metaconid-protoconid except anteriorly. In KU10259 the postentoconid valley is barely open, but the tooth is rather worn, and the metaconid is essentially isolated without either anterior or posterior connections. The mesolophid is generally short and commalike in structure. As far as available specimens are concerned, third molars of *P. (P.) clivosus* and *P. (S.) galbreathi* may be distinguished by the latter never having a posterior connection of any kind between protoconid and metaconid. The tooth may be slightly more reduced, relative to $M_1$-$M_2$, than in *P. (S.) grangeri*; the tooth, relative to others is smaller in *P. (S.) sabrae* (BLACK, 1958, p. 4).

Measurements of *Plesiosminthus (Schaubeumys) galbreathi* have been given under the description of *P. (P.) clivosus*. Those of *P. (S.) grangeri* and most of those of *P. (S.) sabrae* were furnished through the courtesy of Mr. CRAIG BLACK of Harvard University. The others are from published sources. Averages to the nearest tenth of a millimeter of teeth from the collections of *Schaubeumys* are given here for use in the discussion below. Numerals enclosed by parentheses indicate number of specimens measured.

*Measurements of* Plesiosminthus (Schaubeumys), *in Millimeters*

| | *P. (S.) grangeri* (type) (lower Rosebud) | *P. (S.) galbreathi* (Marslandian) | *P. (S.) sabrae* (Sheepcreekian) |
|---|---|---|---|
| $M^1$, ap | ?1.6 | 1.5 (4) | 1.3 (10) |
| tr | ?1.4 | 1.5-(4) | 1.3-(10) |
| $M_1$, ap | 1.6 | 1.5 (7) | 1.3 (3) |
| tr | 1.2 | 1.1 (7) | 1.0 (3) |
| $M_2$, ap | 1.5 | 1.4 (7) | 1.3 (2) |
| tr | 1.2 | 1.2 (8) | 1.1 (2) |

## RELATIONSHIPS OF SCHAUBEUMYS

The close relationship of *Plesiosminthus (Schaubeumys) galbreathi* to the type species, *P. (S.) grangeri*, and to *P. (S.) sabrae*, is obvious. With only a single specimen of *P. (S.) grangeri* available, it is even difficult to establish characters that serve to separate the two species—especially because I think that the more obvious distinctions may be subject to individual variation. Assuming, however, that the type of *P. (S.) grangeri* is not completely atypical, one or more of the characteristics of the formal diagnosis should prove to be specific. *P. (S.) galbreathi* differs from *P. (S.) sabrae* as follows: (1) larger average size; (2) $P^4$ with an obvious principal cusp and smaller cuspule rather than two subequal cusps, the principal one being more nearly median in position than in *P. (S.) sabrae;* (3) lower incisor more compressed, with rounded rather than flattened anterior face; (4) small anteroconid on $M_1$ rather than none; (5) mesolophid in $M_1$-$M_2$ usually longer and continuous with metastylid (mesostylid), rather than separate from metastylid; and (6) mesolophid of $M_3$ not reaching internal margin of tooth rather than extending that far in *P. (S.) sabrae*.

The South Dakota, Wyoming, and Colorado species possibly should be treated as subspecies in a temporal sequence with decreasing size in later kinds. The Split Rock and Quarry A samples are sufficient to suggest a size difference, and extrapolation back indicates that *Plesiosminthus (Schaubeumys) grangeri* may really average somewhat larger, as the one known specimen only faintly suggests. Until an adequate sample of *P. (S.) grangeri* becomes available, I see no advantage to a subspecific arrangement, and many taxonomists in any case prefer to retain the subspecies unit as a geographic one.

The new material again demonstrates that *Plesiosminthus (Schaubeumys)* is a zapodid rather than a cricetid as WOOD (1935a) thought when describing the genus. Proof of zapodid relations is seen in several features of the upper dentition not available in the type specimen: (1) dental formula $\frac{1.0.1.3}{1.0.0.3}$; (2) dipodoid zygomasseteric structure; (3) upper incisors grooved and enamel distributed as in *Plesiosminthus*. STEHLIN & SCHAUB (1951, p. 314) first pointed out the true relations of *P. (S.) grangeri*. Since then WOOD has concurred (1955a, p. 520) with this opinion, and BLACK (1958) has reaffirmed it.

Are *Schaubeumys* and *Plesiosminthus* generically distinct? Although each has its assemblage of typical characters, these characters are not constant. The situation seems to me to be somewhat analogous to that in ground squirrels of the *Citellus* group. Perhaps, as in that, subgeneric treatment is a logical one. In general, *P. (Schaubeumys)* is to be distinguished from *P. (Plesiosminthus)* by a more cuspidate (in contrast to a more crested) type of molar pattern. This is most evident in $M^1/M_1$, and least evident in $M^3/M_3$. There is, however, variation in this regard, individually, with wear, and perhaps specifically in *P. (Plesiosminthus)*. Certain specimens of *P. (P.) myarion*, at least, are more advanced than *P. (P.) clivosus* in degree of compression of protocone and hypocone, and, of protoconid and hypoconid as well. The American species may have a greater resemblance to *P. (P.) schaubi* (type of the genus) in this feature than to *P. (P.) myarion*. The sample from Quarry A is not sufficiently large to satisfy me on the point. The alternative seems to me, to be to refer *P. (S.) galbreathi* also to *Plesiosminthus (Plesiosminthus)*. If oblique compression is to be regarded as an advanced feature, the Aquitanian species is more advanced than the later American one.

A series of characters that seems to depend on this general feature of compression in *Schaubeumys* are: (1) a well-developed anterocone (?protoconule), especially on $M^1$; (2) a well-developed hypoconulid, especially on $M_1$; (3) protocone and hypocone of upper molars more anteroposteriorly than obliquely compressed; (4) paracone of $M^2$ (in the one available specimen) more or less isolated; (5) anterior cingulum of $M^3$ extends linguad. I am impressed with the differences existing between the contemporaneous and presumably coexisting *P. (P.) clivosus and P. (S.) galbreathi*. The generic names, too, are already in the literature. I therefore propose that the "genera" be regarded as subgenera of *Plesiosminthus*.

*Parasminthus* BOHLIN presumably differs from both *Plesiosminthus (Plesiosminthus)* VIRET and *P. (Schaubeumys)* WOOD in the character of the upper incisors, and in root development in upper molars. Otherwise, as BOHLIN (1946) has indicated, there is great resemblance to *Plesiosminthus* (and *Schaubeumys*), although differences in tooth pattern and shape seemingly are present if Bohlin's material is correctly segregated taxonomically, and the isolated teeth correctly assigned as to position in the jaw. As examples of these differences may be cited $M^1$ of *Parasminthus asiae-centralis* (BOHLIN, 1946, fig. 2, 2) which has the posterior lobe of the tooth wider than the anterior, the reverse of *P. (S.) galbreathi*. There is also a rather characteristic posterior union of metacone with hypocone, or more frequently the posteroloph in *Parasminthus asiae-centralis* and *P. tangingola* (fig. 2, 2, 7), which is not seen in *Plesiosminthus* or *Schaubeumys*. The posterior attachment of the metacone is a feature of the Dipodidae (SCHAUB, 1934, fig. 25). Perhaps the relationship is here rather than to the Zapodidae. To me, *P. parvulus* seems a more orthodox plesiosmin*thid* than other species of *Parasminthus*. I am tentatively including *Parasminthus* as a subgenus of *Plesiosminthus* (a possible treatment suggested by BOHLIN, p. 43). Thus, the species may be arranged as follows:

*Subgenera and Species of* Plesiosminthus

| | |
|---|---|
| *Plesiosminthus (Plesiosminthus)* | *schaubi* VIRET |
| | *myarion* SCHAUB |
| | *promyarion* SCHAUB |
| | *clivosus* GALBREATH |
| *Plesiosminthus (Schaubeumys)* | *grangeri* (WOOD) |
| | *galbreathi* WILSON |
| | *sabrae* (BLACK) |
| *Plesiosminthus (Parasminthus)* | asiae-centralis (BOHLIN) |
| | *tangingola* (BOHLIN) |
| | *parvulus* (BOHLIN) |

BLACK (1958), in a discussion of relationships accompanying his description of *Plesiosminthus (Schaubeumys) sabrae*, arrives at a somewhat different arrangement. He assigned not only *P. (S.) sabrae* to *Schaubeumys* (regarded as a full genus), but thought that *P. clivosus* should be so assigned also. He did not think there was sufficient evidence for referring the American species to the European *Plesiosminthus*. He, however, stressed the similarity of the species of *Plesiosminthus, Parasminthus,* and *Schaubeumys* to each other. Perhaps my own arrangement is made under the influence chiefly of two considerations: (1) I find no morphological features that satisfactorily separate *P. clivorus, P. schaubi,* and *P. myarion* at a generic level; and (2) *P. clivosus* is not a unique case at Quarry A in respect to its close relationship to European species.

The Quarry A species and that from Split Rock, Wyoming, represent a later stage in zapodid evolution than species of *Plesiosminthus* and of *Parasminthus* from the Old World. The American species do not, however, help in ascertaining the evolution of the zapodids. A few features are reminiscent of *Pliozapus* (WILSON, 1936, p. 29) of the middle Pliocene, but lack of closure of the postentoconid valleys in *Pliozapus* even with heavy wear (WILSON, *op. cit.*, pl. 2, fig. 4a) seemingly prevents consideration of the Pliocene genus as a direct descendant of the older American species. *Macrognathomys* HALL

(1930, p. 305, figs. 13, 14), although a zapodid, is obviously not closely related to any of the other fossil genera, and seems closer to *Sicista* than to *Pliozapus* if illustrated correctly.

Certainly the growing number of zapodid fossils permits us to hope that eventually a reasonable phylogeny may be constructed for this group. I suspect, also, that there is more zapodid material in American collections than is evident from the literature. Even in named species, there has been consistent confounding with the Cricetidae, and in rapidly curated collections the chances seem high for this kind of error.

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